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**The Analysis of Structured Population on Two
Patches and Some Second-Order Transcendental
Equations**

by

Masky Ka Yu Ng



A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of Master of Science

in

Applied Mathematics

Department of Mathematical and Statistical Sciences

Edmonton, Alberta
Fall 2003



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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **The Analysis of Structured Population on Two Patches and Some Second Order Transcendental Equations** submitted by **Masky Ka Yu Ng** in partial fulfillment of the requirements for the degree of Master of Science in Applied Mathematics.

Abstract

In this thesis, we formulate and analyze the dynamics of a single species population with both spatial dispersal (over two patches) and time delay (arising from the maturation period). Three different models are being considered. The first model is to restrict the migration between the two patches to one-way. We look at the stability of the model and show the existence of periodic solutions. Next we consider a model which has zero growth rate in one of the patches and a model in which the immature population is immobile. Stability analysis of both models lead to some rather difficult and interesting second-order transcendental equations, especially for the third model. A detail analysis for such transcendental equations is provided, including a method to determine whether all their roots lie on the left half of the complex plane. Finally, we do some numerical simulations for all three models.

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1 Introduction. Structured Population in a Patchy Environment

Let $u(t)$ be the population density of a single species population in a homogeneous environment. If we denote its (constant) death rate by δ and its birth function by $b(u)$, then the dynamics of this population will be given by the simple ordinary differential equation (ODE)

$$\frac{du(t)}{dt} = -\delta u(t) + b(u(t)). \quad (1)$$

However, if one considers various factors causing delayed growth response, such as hatching period, duration of gestation, maturation delay and slow replacement of food consumed, then it becomes necessary to add a time delay $r > 0$ to (1), resulting in some form of delay differential equations. The books by Cushing [1977], Kuang [1993], MacDonald [1979], and May [1974,1981] summarized the theoretical advance and application background for models for population growth involving delays. A particularly simple case would be to assume that the population is divided into two age classes: immature and mature. Let $w(t)$ denote the mature population. Then

$$\frac{dw(t)}{dt} = -d_m w(t) + e^{-d_I r} b(w(t-r)), \quad (2)$$

where d_m is the death rate of the mature population, r is the maturation period and d_I is the death rate of the immature population. The term $b(w(t-r))$ involves the value of the mature population at time $t-r$ since only those infants born at time r units ago become mature at time t . The factor $e^{-d_I r}$ is needed here since not all infants can grow up to maturity, where d_I is the death rate of the immature population. Such an equation (2) is called a *delay differential equation* (DDE) or a *functional differential equation* (FDE) [15].

In this thesis, we will combine both spatial and temporal heterogeneities, ignored in model equation (1). Following So, Wu and Zou [2001a], a model of a single species living in a n -patch environment can be developed as follows. Let $u_i(t, a)$ denote the number of the species in patch i ($i = 1, 2, \dots, n$), at time t ($t > 0$), and at age a ($0 \leq a < \infty$). According to Diekmann and Metz [1986], one has the following hyperbolic equation for structured population:

$$\frac{\partial u_i(t, a)}{\partial t} + \frac{\partial u_i(t, a)}{\partial a} = -d_i(a)u_i(t, a) + \sum_{j=1}^n D_{ij}(a)u_j(t, a). \quad (3)$$

Here $d_i(a)$ is the death rate of individuals of age a in patch i and $D_{ij}(a)u_j(t, a)$ ($j \neq i$) corresponds to the dispersal of individuals of age a from patch j to patch i .

Note that $D_{jj}(a) \leq 0$ is the rate of emigrating (exiting) from patch j , irrespective of where the individual ends up. Thus, for a fixed j , $\sum_{i=1}^n D_{ij}(a) \leq 0$, with equality “=” if we assume that there is no loss of life during migration.

Suppose now that the population consists of two age-structured classes: immature and mature, and denote the maturation age by $r \geq 0$. For $i = 1, \dots, n$, we assume that

$$d_i(a) = \begin{cases} d_{i,I}(a), & \text{for } 0 \leq a \leq r, \\ d_{i,m}, & \text{for } a > r \end{cases}$$

and

$$D_{ij}(a) = \begin{cases} D_{ij,I}(a), & \text{for } 0 \leq a \leq r, \\ D_{ij,m}, & \text{for } a > r \end{cases}$$

where $d_{i,m}$, $D_{ij,m}$ are constants, I stands for immature/infant and m stands for mature/adult. At a given time t , the number of adults in patch i is given by

$$w_i(t) = \int_r^\infty u_i(t, a) da.$$

Since only adults can give birth, the number of newborns at time t is given by

$$u_i(t, 0) = b_i(w_i(t)), \quad (4)$$

where $b_i(w) \geq 0$ is the birth function of the specie in patch i . By integrating (3) with respect to a from r to ∞ , we have

$$\begin{aligned} \frac{d}{dt} w_i(t) &= - \int_r^\infty \frac{\partial u_i}{\partial a}(t, a) da - \int_r^\infty d_i(a) u_i(t, a) da + \int_r^\infty \sum_{j=1}^n D_{ij}(a) u_j(t, a) da \\ &= u_i(t, r) - d_{i,m} w_i(t) + \sum_{j=1}^n D_{ij,m} w_j(t), \end{aligned} \quad (5)$$

where we have assumed $u_i(t, \infty) = 0$, i.e. no individual lives forever.

Next, we need to derive a formula for $u_i(t, r)$. To do that, we will integrate along characteristics. Fix s and consider the function

$$V_i^s(t) = u_i(t, t-s), \quad \text{for } s \leq t \leq s+r.$$

Then

$$\frac{d}{dt} V_i^s(t) = -d_i(t-s) V_i^s(t) + \sum_{j=1}^n D_{ij}(t-s) V_j^s(t). \quad (6)$$

Now if we further assume that

$$d_i(a) = d_{i,I} > 0, \quad \text{for } 0 \leq a \leq r$$

and

$$D_{ij}(a) = D_{ij,I} > 0, \quad \text{for } 0 \leq a \leq r,$$

where $d_{i,I}$ and $D_{ij,I}$ are constants, then (6) becomes a system of linear (ODE)s of constant coefficients:

$$\frac{d}{dt}V_i^s(t) = -d_{i,I}V_i^s(t) + \sum_{j=1}^n D_{ij,I}V_j^s(t).$$

Define the matrices

$$\begin{aligned} M_I &= -\text{diag}(d_{i,I})_{i=1}^n + [D_{ij,I}], \\ M_m &= -\text{diag}(d_{i,m})_{i=1}^n + [D_{ij,m}]. \end{aligned}$$

Note that M_I and M_m are $n \times n$ matrix with non-negative off-diagonal entries and negative column sums. Since

$$\frac{d}{dt}V^s(t) = M_I V^s(t),$$

where $V^s = (V_1^s, \dots, V_n^s)^T$, therefore

$$V^s(t) = e^{M_I(t-s)}V^s(s) = e^{M_I(t-s)}b(w(s)),$$

and

$$u(t, r) = V^{t-r}(t) = e^{M_I r}b(w(t-r)), \quad (7)$$

where $u(t, r) = (u_1(t, r), \dots, u_n(t, r))^T$ and $b(w(t-r)) = (b_1(w_1(t-r)), \dots, b_n(w_n(t-r)))^T$. Combining (5) and (7), we get

$$w'(t) = M_m w(t) + e^{M_I r}b(w(t-r)), \quad (8)$$

where $w = (w_1, \dots, w_n)^T$.

According to the way we formulate our model, it is reasonable to expect that if the birth functions are bounded, any solution of (8) with a non-negative initial condition is bounded and stays non-negative. Therefore, we have the following theorems.

Theorem 1.1 *If $\phi \in C([-r, 0], \mathbb{R}^n)$ such that $\phi(\theta) \geq 0$, $-r \leq \theta \leq 0$, then the solution $w(t, \phi)$ of (8) must be non-negative. Moreover, it is bounded for all $t \geq 0$ if the birth functions are bounded.*

Before we prove this theorem, we need the following lemma.

Lemma 1.1 *Suppose an $n \times n$ matrix M has non-negative off-diagonal entries, then all the entries of e^M must be non-negative.*

Proof: Suppose

$$M = \begin{bmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{bmatrix},$$

where $a_{ij} \geq 0$, when $i \neq j$. We let $a = \min\{a_{ii} \mid i = 1, \dots, n\}$ and define

$$D = \begin{bmatrix} a & 0 & \cdots & 0 \\ 0 & a & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & a \end{bmatrix}$$

and

$$\hat{M} = \begin{bmatrix} a_{11} - a & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} - a & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} - a \end{bmatrix}.$$

Then, it is clear that $M = D + \hat{M}$. Also, since D and $\hat{M}$ commute, we must have

$$e^M = e^D e^{\hat{M}}.$$

Thus, the claim follows since all the entries of $\hat{M}$ are non-negative and e^D is a diagonal matrix with all the diagonal entries equal to e^a .

□

Proof of Theorem 1.1: For convenience, we let $f(w) : C[-r, 0] \rightarrow \mathbb{R}^n$ be the right hand side of equation (8). First, we look at the first part of the theorem. If we can apply Theorem A.1 in the appendix, we see that the claim follows immediately. Thus, we only need to verify that the condition

$$\text{if } \phi \geq 0, \quad \phi_i(0) = 0 \quad \text{for some } i, \quad \text{then } f_i(\phi) \geq 0$$

is true. But, since M_I is a matrix with non-negative off-diagonal entries, it follows from the previous lemma that all the entries of $e^{M_I r}$ are non-negative. Then, since M_m is also a matrix with non-negative off-diagonal entries and the birth function $b(w)$ is non-negative. Therefore, the condition is guaranteed. This proves the first part of the theorem.

To prove the second part of the theorem, we define

$$u(t) = w_1(t) + w_2(t) + \cdots + w_n(t).$$

Then, we have

$$u'(t) = -\sum_{i=1}^n p_i w_i(t) + \sum_{i=1}^n q_i b_i(w_i(t-r)),$$

where $p_i > 0$ and $q_i \geq 0$, since M_m has negative column sums and all the entries of $e^{M_I r}$ are non-negative.

Now, since the birth functions $b_i(w)$, $i = 1, \dots, n$ are bounded, we let B be a common upper bound of these functions. Also, we let $p = \min\{p_i \mid i = 1, \dots, n\}$ and $q = \max\{q_i \mid i = 1, \dots, n\}$. Then,

$$\begin{aligned} u'(t) &\leq -p \sum_{i=1}^n w_i(t) + nqB \\ &\leq -pu(t) + nqB, \end{aligned}$$

when $w_i(t) \geq 0$, for $i = 1, \dots, n$. We see that $u'(t) < 0$ when $u(t) > \frac{nqB}{p}$. Thus, combining this with the first part of the theorem, we can conclude that any solution of (8) with a non-negative initial condition is bounded.

□

The objective of this thesis is to analyze model equation (8) for several special cases. In fact, we will only study the two patch case (i.e. $n = 2$) and a typical birth function we will use is

$$b_i(w) = p_i w e^{-\beta_i w},$$

where $p_i > 0$ and $\beta_i > 0$ [15]. The reader can consult Appendix C for properties of the function $b(w) = p w e^{-\beta w}$. The two patch case with identical patch dynamics had been considered in So, Zou and Wu [2001a]. In this thesis, we wish to consider cases when the two patches may not be identical. It turns out we will encounter some interesting second order transcendental equations which had not been considered before in the literature. In Section 2, we discuss the case of one way migration, that is, individuals will only go from patch 2 to patch 1 but not vice versa. We consider the equilibria of this system, their stability and Hopf bifurcations. In Section 3, we study second order transcendental equations that will arise from the models in Section 4 and 5. We obtain necessary and sufficient conditions for the roots of such transcendental equation to remain on the left half plane. In Section 4, we consider the case when the growth function in one of the patches is zero. Again, equilibria and their stability are considered. In Section 5, we consider the case when the immature population is immobile. We show that the positive equilibrium is unique. The

characteristic equation is quite complex in this case, since there are two different exponential terms. We will treat it using two approaches, each of which gives partial results to the stability problem. Finally, we use DDE23 in Section 6 to integrate (8) numerically and compare the numerical results with the analytic result in Section 2, Section 4 and Section 5.

2 One-Way Migration

2.1 Model Equations

In this section, we will consider a two patch environment and we assume that individuals in patch 1 will not migrate to patch 2. In addition, for simplicity, we also assume that the total loss rate (i.e. death rate plus dispersal rate) of the immature is patch independent. Consequently,

$$\begin{cases} D_{21,I} &= 0, \\ D_{21,m} &= 0, \\ -d_{1,I} + D_{11,I} &= -d_{2,I} + D_{22,I}. \end{cases}$$

Thus,

$$M_I = \begin{bmatrix} -L & D_{12,I} \\ 0 & -L \end{bmatrix},$$

and

$$M_m = \begin{bmatrix} -D_1^* & D_{12,m} \\ 0 & -D_2^* \end{bmatrix}.$$

where $L = d_{1,I} - D_{11,I} = d_{2,I} - D_{22,I}$, $D_1^* = d_{1,m} - D_{11,m}$, and $D_2^* = d_{2,m} - D_{22,m}$. Note that $L, D_1^*, D_2^* > 0$, $D_{12,I}, D_{12,m} \geq 0$. We also assume that $D_{12,I} + D_{12,m} > 0$.

Our model equation (8) becomes

$$w'(t) = \begin{bmatrix} -D_1^* & D_{12,m} \\ 0 & -D_2^* \end{bmatrix} w(t) + \begin{bmatrix} e^{-Lr} & e^{-Lr} D_{12,I} r \\ 0 & e^{-Lr} \end{bmatrix} b(w(t-r)),$$

or equivalently,

$$w_1'(t) = -D_1^* w_1(t) + D_{12,m} w_2(t) + e^{-Lr} b_1(w_1(t-r)) + e^{-Lr} D_{12,I} r b_2(w_2(t-r)), \quad (9)$$

$$w_2'(t) = -D_2^* w_2(t) + e^{-Lr} b_2(w_2(t-r)). \quad (10)$$

2.2 Equilibria

In this subsection, we concentrate on the non-negative equilibria of (9)-(10).

The equilibrium equations are:

$$D_1^* w_1 = D_{12,m} w_2 + e^{-Lr} b_1(w_1) + e^{-Lr} D_{12,I} r b_2(w_2), \quad (11)$$

$$D_2^* w_2 = e^{-Lr} b_2(w_2). \quad (12)$$

Now looking at (12), we get

$$D_2^* w_2 = e^{-Lr} p_2 w_2 e^{-\beta_2 w_2}. \quad (13)$$

So, as long as $w_2 \neq 0$, we have,

$$\begin{aligned} D_2^* e^{Lr} &= p_2 e^{-\beta_2 w_2} \\ w_2 &= \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*}. \end{aligned}$$

Thus, at an equilibrium, we must have $w_2 = 0$ or $w_2 = \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*}$. Since we are interested in the possibility of existence of positive equilibrium, we will assume from now on that $\frac{p_2 e^{-Lr}}{D_2^*} > 1$.

If we substitute $w_2 = 0$ into (11), we get

$$\begin{aligned} D_1^* w_1 &= e^{-Lr} p_1 w_1 e^{-\beta_1 w_1} \\ w_1 &= \beta_1^{-1} \ln \frac{p_1 e^{-Lr}}{D_1^*} \end{aligned} \quad (14)$$

so that $w_1 = 0$ or $w_1 = \beta_1^{-1} \ln \frac{p_1 e^{-Lr}}{D_1^*}$. Again since we are interested in the existence of positive equilibrium, we will assume from now on that $\frac{p_1 e^{-Lr}}{D_1^*} > 1$.

On the other hand, if we substitute $w_2 = \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*}$ into (11), we obtain

$$\begin{aligned} D_1^* w_1 &= e^{-Lr} b_1(w_1) + D_{12,m} \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*} + D_{12,I} D_2^* r \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*} \\ &= e^{-Lr} b_1(w_1) + \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*} [D_{12,m} + D_{12,I} D_2^* r] \\ D_1^* w_1 &= e^{-Lr} b_1(w_1) + M, \end{aligned} \quad (15)$$

where $M = \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*} [D_{12,m} + D_{12,I} D_2^* r]$. Since $M > 0$ and is independent of w_1 , according to Appendix C, (15) must have one and only one positive solution. We will call it w^* , where $w^* > 0$.

Thus, we have

Theorem 2.1 *If $D_1^* < p_1 e^{-Lr}$ and $D_2^* < p_2 e^{-Lr}$, the non-negative equilibria of (9)-(10) are:*

$$E_0 = (0, 0) \quad , \quad E_1 = (\bar{w}_1, 0) \quad \text{and} \quad E_2 = (w^*, \bar{w}_2),$$

where $\bar{w}_i = \beta_i^{-1} \ln \frac{p_i}{e^{Lr} D_i^*}$ and w^* is the unique positive solution of (15).

2.3 Stability

The stability of an equilibrium $(\hat{w}_1, \hat{w}_2)$ is determined by the roots of its characteristic equation. To be precise, an equilibrium is asymptotically stable if all roots of its characteristic equation have negative real parts; and it is unstable if there is a root that has a positive real part [2]. The characteristic equation is obtained by linearizing (9)-(10) about $(\hat{w}_1, \hat{w}_2)$ and then plug in a non-trivial solution $(w_1, w_2) = (\xi_1 e^{\lambda t}, \xi_2 e^{\lambda t})$:

$$\begin{aligned} 0 &= \begin{vmatrix} \lambda + D_1^* - e^{-Lr} b_1'(\hat{w}_1) e^{-\lambda r} & -D_{12,m} - e^{-Lr} D_{12,I} r b_2'(\hat{w}_2) e^{-\lambda r} \\ 0 & \lambda + D_2^* - e^{-Lr} b_2'(\hat{w}_2) e^{-\lambda r} \end{vmatrix} \\ &= [\lambda + D_1^* - e^{-Lr} b_1'(\hat{w}_1) e^{-\lambda r}] [\lambda + D_2^* - e^{-Lr} b_2'(\hat{w}_2) e^{-\lambda r}] \end{aligned}$$

so that

$$0 = \lambda + D_1^* - e^{-Lr} b_1'(\hat{w}_1) e^{-\lambda r} \tag{16}$$

or

$$0 = \lambda + D_2^* - e^{-Lr} b_2'(\hat{w}_2) e^{-\lambda r}. \tag{17}$$

Notice that both (16) and (17) are of the form

$$0 = \lambda + A + B e^{-\lambda r}. \tag{18}$$

Necessary and sufficient conditions for all roots of (18) to have negative real parts are well known, see Bellman and Cooke [1963]. This Theorem is recalled in Appendix B.

After multiplying (16) and (17) by $r e^{\lambda r}$ and set $z = \lambda r$, we can apply Theorem B.1 and get the following conclusions:

All the roots of equation (16) have negative real parts if and only if the following conditions are satisfied:

1. $D_1^* r > -1$;
2. $D_1^* > e^{-Lr} b_1'(\hat{w}_1)$;

3. $-e^{-Lr}rb'_1(\hat{w}_1) < \sqrt{v(-D_1^*r)^2 + (D_1^*r)^2}$, where $v(x)$ is the unique root of $v \cot v = x$, for $v \in (0, \pi)$.

All the roots of equation (17) have negative real parts if and only if the following conditions are satisfied:

4 $D_2^*r > -1$;

5 $D_2^* > e^{-Lr}b'_2(\hat{w}_2)$;

- 6 $-e^{-Lr}rb'_2(\hat{w}_2) < \sqrt{v(-D_2^*r)^2 + (D_2^*r)^2}$, where $v(x)$ is the unique root of $v \cot v = x$, for $v \in (0, \pi)$.

Note: Condition (1) and (4) always hold.

Clearly

$$b'_i(w) = p_i e^{-\beta_i w} (1 - \beta_i w).$$

At $E_0 = (0, 0)$, we have $\hat{w}_1 = 0$ and $\hat{w}_2 = 0$. Since

$$b'_1(0) = p_1 \quad \text{and} \quad b'_2(0) = p_2,$$

and by assumption

$$D_1^* < e^{-Lr}p_1 \quad \text{and} \quad D_2^* < e^{-Lr}p_2,$$

therefore (16) and (17) both have positive (real) roots. Thus, E_0 is always **unstable** as long as a non-trivial equilibrium exists.

At $E_1 = (\bar{w}_1, 0)$, we have $\hat{w}_1 = \bar{w}_1$ and $\hat{w}_2 = 0$. Since equation (17) must have a root with positive real part due to

$$D_2^* < e^{-Lr}p_2,$$

E_1 is also always **unstable**.

At $E_2 = (w^*, \bar{w}_2)$, we have $\hat{w}_1 = w^*$ and $\hat{w}_2 = \bar{w}_2$. Since w^* is the unique positive solution of equation (15), therefore,

$$D_1^* > e^{-Lr}b'_1(w^*).$$

According to the above, all roots of (16) have negative real part iff

$$-e^{-Lr}rb'_1(w^*) < \sqrt{v(-D_1^*r)^2 + (D_1^*r)^2}. \quad (19)$$

Similarly, since $\bar{w}_2$ is the unique positive solution of equation (13), we must have

$$D_2^* > e^{-Lr} b'_2(\bar{w}_2).$$

Therefore, all roots of (17) have negative real part iff

$$-e^{-Lr} r b'_2(\bar{w}_2) < \sqrt{v(-D_2^* r)^2 + (D_2^* r)^2}. \quad (20)$$

Consequently, E_2 is asymptotically stable if conditions (19) and (20) are satisfied.

Remark: Conditions (19) and (20) are certainly feasible. Consider the case when, $1 < \frac{p_1 e^{-Lr}}{D_1^*} < e^2$ and $1 < \frac{p_2 e^{-Lr}}{D_2^*} < e^2$. By the properties of the function $b_i(w)$, for $w > 0$, conditions (19) and (20) are guaranteed. On the other hand, since $e^{-Lr} r b'_2(\bar{w}_2) = D_2^* r \left(1 - \ln \frac{p_2}{e^{Lr} D_2^*} \right)$, so if we choose p_2 to be sufficiently large while keeping the other parameters unchanged, we can make condition (20) fail.

Summarizing the above discussion, we have

Theorem 2.2 *If all the non-negative equilibria E_0 , E_1 , and E_2 exist, i.e. $D_i^* < p_i e^{-Lr}$ ($i = 1, 2$), then*

- (i) E_0 and E_1 are unstable, and,
- (ii) E_2 is asymptotically stable if conditions (19) and (20) are satisfied.

2.4 Bifurcation Analysis

In this section, we will show that under certain conditions, Hopf bifurcation can occur at the two non-trivial equilibria, E_1 and E_2 , and thus existence of periodic solutions. We should keep in mind that the conditions $D_1^* < p_1 e^{-Lr}$ and $D_2^* < p_2 e^{-Lr}$ have to remain valid in order for E_1 and E_2 to exist. Therefore, we have to be extra careful when a bifurcation parameter is involved in these terms.

Hopf Bifurcation at E_1

For the equilibrium $E_1 = (\bar{w}_1, 0) = (\beta_1^{-1} \ln \frac{p_1 e^{-Lr}}{D_1^*}, 0)$, we use L (c.f. Section 2.1) as the bifurcation parameter. Let us do the bifurcation analysis along the w_1 -direction and look at the characteristic equation (16), which is

$$\lambda + D_1^* - e^{-Lr} b_1'(\bar{w}_1) e^{-\lambda r} = 0. \quad (21)$$

Assume that $\lambda = iy$, $y > 0$ is a characteristic root such that it satisfies (21) when $L = \hat{L}$. Thus, we must have

$$D_1^* - e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L})) \cos(ry) = 0, \quad (22)$$

$$y + e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L})) \sin(ry) = 0. \quad (23)$$

In fact (22) is equivalent to

$$ry = \cos^{-1} \left(\frac{D_1^*}{e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L}))} \right), \quad (24)$$

and (22) and (23) together imply

$$y = \sqrt{[e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L}))]^2 - D_1^{*2}}. \quad (25)$$

Thus,

$$r \sqrt{[e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L}))]^2 - D_1^{*2}} = \cos^{-1} \left(\frac{D_1^*}{e^{-\hat{L}r} b_1'(\bar{w}_1(\hat{L}))} \right). \quad (26)$$

Recall $e^{-Lr} b_1'(\bar{w}_1(L)) = D_1^* \left(1 - \ln \frac{p_1 e^{-Lr}}{D_1^*} \right)$. So, by this we can tell immediately that (25) is defined only if $\frac{p_1 e^{-\hat{L}r}}{D_1^*} > e^2$. Therefore, we can see that Hopf Bifurcation at E_1 is not possible in the w_1 -direction if $\frac{p_1}{D_1^*} \leq e^2$. From now on, we will assume that $\frac{p_1}{D_1^*} > e^2$.

Define the two functions

$$f(L) = r \sqrt{[e^{-Lr} b_1'(\bar{w}_1(L))]^2 - D_1^{*2}}$$

and

$$g(L) = \cos^{-1} \left(\frac{D_1^*}{e^{-Lr} b_1'(\bar{w}_1(L))} \right).$$

It is easy to see that $f(L)$ and $g(L)$ are only defined on $I = [0, \alpha]$, where $\alpha = \frac{1}{r} \ln \frac{p_1}{D_1^* e^2}$. Also, $L \mapsto [e^{-Lr} b_1'(\bar{w}_1(L))]^2$ is a decreasing function in L on the interval I . This implies that $f(L)$ is a decreasing function on I with $f(\alpha) = 0$ and $g(L)$ is an increasing function on I with $g(\alpha) = 2k\pi + \pi$ in the range $[2k\pi + \pi/2, 2k\pi + \pi]$, $k = 0, 1, 2, \dots$.

Knowing this, we see that equation $f(L) = g(L)$ has $(k' + 1)$ solutions on the interval I if $f(0) > g(0) \in [2k'\pi + \pi/2, 2k'\pi + \pi]$. Thus, by (26), there are $(k' + 1)$ possible bifurcation values if

$$r > \frac{\cos^{-1} \left((1 - \ln \frac{p_1}{D_1^*})^{-1} \right)}{\sqrt{(D_1^* (1 - \ln \frac{p_1}{D_1^*}))^2 - D_1^{*2}}},$$

where the range of $\cos^{-1}$ is taken to be $[2k'\pi + \pi/2, 2k'\pi + \pi]$.

Note: (23) rules out the need for considering $g(L)$ in the range of $[2k\pi + \pi, 2k\pi + 3\pi/2]$, $k=0,1,\dots$.

Next, we need to check the transversality condition.

Substitute $\lambda = x + iy$ into (21) and separate it into real and imaginary parts, we get

$$Re : \quad x + D_1^* = e^{-Lr} b_1'(\bar{w}_1(L)) e^{-rx} \cos ry, \quad (27)$$

$$Im : \quad y = -e^{-Lr} b_1'(\bar{w}_1(L)) e^{-rx} \sin ry. \quad (28)$$

Dividing (28) by (27), we get

$$-y = (x + D_1^*) \tan ry.$$

Differentiate it with respect to L , one gets

$$-\frac{dy}{dL} = \frac{dx}{dL} \tan ry + (x + D_1^*) (1 + \tan^2 ry) r \frac{dy}{dL}.$$

Assuming that $L = \hat{L}$ is a bifurcation value, then

$$\left. \frac{dy}{dL} \right|_{L=\hat{L}} = \frac{-\tan ry}{1 + D_1^* r (1 + \tan^2 ry)} \left. \frac{dx}{dL} \right|_{L=\hat{L}}. \quad (29)$$

Also, $(27)^2 + (28)^2$ gives us

$$\begin{aligned}(x + D_1^*)^2 + y^2 &= [e^{-Lr}b_1'(\bar{w}_1(L))e^{-rx}]^2 \\ &= \left[D_1^* \left(1 - \ln \frac{p_1 e^{-Lr}}{D_1^* e^{-rx}} \right) \right]^2.\end{aligned}$$

Differentiating this with respect to L and setting $L = \hat{L}$, we get

$$D_1^* \left[1 - r \left(1 - \ln \frac{p_1 e^{-\hat{L}r}}{D_1^*} \right) \right] \frac{dx}{dL} \Big|_{L=\hat{L}} + y \frac{dy}{dL} \Big|_{L=\hat{L}} = D_1^{*2} r \left(1 - \ln \frac{p_1 e^{-\hat{L}r}}{D_1^*} \right) \quad (30)$$

According to (29), $\frac{dy}{dL} \Big|_{L=\hat{L}} = 0$ if and only if $\frac{dx}{dL} \Big|_{L=\hat{L}} = 0$. Since the right hand side of (30) is never equal to 0, therefore $\frac{dx}{dL} \Big|_{L=\hat{L}} \neq 0$.

Hopf Bifurcation at E_2

For the equilibrium $E_2 = (w^*, \bar{w}_2) = (w^*, \beta_1^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*})$, we use p_2 as the bifurcation parameter.

Let us do the bifurcation analysis along the w_1 -direction first and look at the characteristic equation (16), which is

$$\lambda + D_1^* - e^{-Lr}b_1'(w^*)e^{-\lambda r} = 0. \quad (31)$$

First, we see that since w^* is the unique positive solution of (15), which is

$$D_1^* w^* = e^{-Lr}b_1(w^*) + \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*} [D_{12,m} + D_{12,I} D_2^* r], \quad (32)$$

therefore w^* depends on p_2 . In particular, w^* increases as p_2 increases. So, we should write $w^*(p_2)$.

As before, we try the pure imaginary root $\lambda = iy$ on (31) assuming $\hat{p}_2$ is a bifurcation value and do the standard analysis. We obtain:

$$ry = \cos^{-1} \left(\frac{D_1^*}{e^{-Lr}b_1'(w^*(\hat{p}_2))} \right), \quad (33)$$

$$\text{and } y = \sqrt{[e^{-Lr}b_1'(w^*(\hat{p}_2))]^2 - D_1^{*2}}. \quad (34)$$

Thus,

$$r \sqrt{[e^{-Lr}b_1'(w^*(\hat{p}_2))]^2 - D_1^{*2}} = \cos^{-1} \left(\frac{D_1^*}{e^{-Lr}b_1'(w^*(\hat{p}_2))} \right). \quad (35)$$

Define the functions

$$f(p_2) = r\sqrt{[e^{-Lr}b'_1(w^*(p_2))]^2 - D_1^{*2}}$$

and

$$g(p_2) = \cos^{-1} \left(\frac{D_1^*}{e^{-Lr}b'_1(w^*(p_2))} \right).$$

As before, by (34), we must have $\frac{p_1 e^{-Lr}}{D_1^*} > e^2$ in order for Hopf bifurcation to be possible. So, we will assume this. Let $m_1 > 0$ be the real number such that

$$\frac{m_1 e^{-Lr}}{D_2^*} = 1.$$

Claim: There exists a real number $m_2 > m_1$ such that the function $f(p_2)$ is well defined on $I = [m_1, m_2]$ with $f(m_2) = 0$ and $f(p_2)$ is decreasing on I .

Proof of Claim: Observe that $w^*(m_1) = \bar{w}_1 = \beta_1^{-1} \ln \frac{p_1 e^{-Lr}}{D_1^*}$ by (32). Using the assumption $\frac{p_1 e^{-Lr}}{D_1^*} > e^2$ and the fact that w^* increases as p_2 increases, one should see that $f(m_1)$ is well defined and the function $f(p_2)$ is actually decreasing. Finally, the existence of m_2 is just a consequence.

As a result, $g(p_2)$ is an increasing function on $[m_1, m_2]$ in the range $[2k\pi + \pi/2, 2k\pi + \pi]$, $k = 0, 1, \dots$, with $g(m_2) = 2k\pi + \pi$. Therefore, we can have $(k' + 1)$ possible bifurcation values if $f(m_1) > g(m_1) \in [2k'\pi + \pi/2, 2k'\pi + \pi]$, or equivalently,

$$r > \frac{\cos^{-1} \left((1 - \ln \frac{p_1 e^{-Lr}}{D_1^*})^{-1} \right)}{\sqrt{(D_1^* (1 - \ln \frac{p_1 e^{-Lr}}{D_1^*}))^2 - D_1^{*2}}}, \quad (36)$$

where the range of $\cos^{-1}$ is taken to be $[2k'\pi + \pi/2, 2k'\pi + \pi]$.

Note: This is possible. Consider keeping $Lr = \text{constant}$ while increasing r .

Next we check the transversality condition.

Let $\lambda = x + iy$ be a root of (21) and assume that $\hat{p}_2$ is a bifurcation value, we get:

$$Re: \quad x + D_1^* = e^{-Lr}b'_1(w^*(p_2))e^{-rx} \cos ry, \quad (37)$$

$$Im: \quad y = -e^{-Lr}b'_1(w^*(p_2))e^{-rx} \sin ry. \quad (38)$$

As before, divide (38) by (37) and differentiate that with respect to p_2 and set $p_2 = \hat{p}_2$, we have

$$\left. \frac{dy}{dp_2} \right|_{p_2=\hat{p}_2} = \frac{-\tan ry}{1 + D_1^* r (1 + \tan^2 ry)} \left. \frac{dx}{dp_2} \right|_{p_2=\hat{p}_2}. \quad (39)$$

Also, $(37)^2 + (38)^2$ gives us

$$(x + D_1^*)^2 + y^2 = [e^{-Lr} b_1'(w^*(p_2)) e^{-rx}]^2.$$

Differentiating this with respect to L and setting $p_2 = \hat{p}_2$, we get

$$\begin{aligned} & [D_1^* + (e^{-Lr} b_1'(w^*(\hat{p}_2)))^2 r] \left. \frac{dx}{dp_2} \right|_{p_2=\hat{p}_2} + y \left. \frac{dy}{dp_2} \right|_{p_2=\hat{p}_2} \\ &= e^{-2Lr} b_1'(w^*(\hat{p}_2)) b_1''(w^*(\hat{p}_2)) \left. \frac{dw^*}{dp_2} \right|_{p_2=\hat{p}_2}. \end{aligned} \quad (40)$$

Note: $b_1'(w^*(\hat{p}_2)) < 0$ and $b_1''(w^*(\hat{p}_2)) > 0$ because of the assumption $\frac{p_1 e^{-Lr}}{D_1^*} > e^2$.

So, we just need to show $\left. \frac{dw^*}{dp_2} \right|_{p_2=\hat{p}_2} \neq 0$. Since w^* is the root of (15), this means

$$D_1^* w^* - e^{-Lr} b_1(w^*) = \beta_2^{-1} \ln \frac{p_2}{e^{Lr} D_2^*} [D_{12,m} + D_{12,I} D_2^* r].$$

Differentiating this with respect to p_2 , we get

$$[D_1^* - e^{-Lr} b_1'(w^*(p_2))] \frac{dw^*}{dp_2} = \frac{1}{\beta_2 p_2} [D_{12,m} + D_{12,I} D_2^* r].$$

Therefore, $\left. \frac{dw^*}{dp_2} \right|_{p_2=\hat{p}_2} \neq 0$ and hence $\left. \frac{dx}{dp_2} \right|_{p_2=\hat{p}_2} \neq 0$, by (39) and (40).

Next, let us do the bifurcation analysis on the w_2 -direction, we look at the characteristic equation (17), which is

$$\lambda + D_2^* - e^{-Lr} b_2'(\bar{w}_2) e^{-\lambda r} = 0. \quad (41)$$

Recall that $\bar{w}_2(p_2) = \beta_2^{-1} \ln \frac{p_2 e^{-Lr}}{D_2^*}$ and $e^{-Lr} b_2'(\bar{w}_2) = D_2^* \left(1 - \ln \frac{p_2 e^{-Lr}}{D_2^*} \right)$.

Again, we try the pure imaginary root $\lambda = iy$ on (41) assuming $\hat{p}_2$ is a bifurcation value and we get:

$$\begin{aligned} ry &= \cos^{-1} \left(\frac{D_2^*}{e^{-Lr} b_1'(\bar{w}_2(\hat{p}_2))} \right), \\ y &= \sqrt{(e^{-Lr} b_2'(\bar{w}_2(\hat{p}_2)))^2 - D_2^{*2}}. \end{aligned}$$

Thus,

$$r \sqrt{(e^{-Lr} b_2'(\bar{w}_2(\hat{p}_2)))^2 - D_2^{*2}} = \cos^{-1} \left(\frac{D_2^*}{e^{-Lr} b_2'(\bar{w}_2(\hat{p}_2))} \right). \quad (42)$$

Define the functions

$$\begin{aligned} f(p_2) &= r \sqrt{(e^{-Lr} b_2'(\bar{w}_2(p_2)))^2 - D_2^{*2}} \\ &= r \sqrt{(D_2^* \left(1 - \ln \frac{p_2 e^{-Lr}}{D_2^*}\right))^2 - D_2^{*2}}, \end{aligned}$$

and

$$g(p_2) = \cos^{-1} \left(\frac{D_2^*}{e^{-Lr} b_2'(\bar{w}_2(p_2))} \right).$$

Clearly, $f(p_2)$ is only defined on $I = [m_1 e^2, \infty)$, where m_1 is the number such that $\frac{m_1 e^{-Lr}}{D_2^*} = 1$. Moreover $f(p_2)$ increases to infinity (i.e. $\lim_{p_2 \rightarrow \infty} f(p_2) = \infty$).

The function $g(p_2)$ is decreasing and is defined on I such that $\lim_{p_2 \rightarrow \infty} g(p_2) = 2k\pi + \pi/2$, if $g(p_2) \in [2k\pi + \pi/2, 2k\pi + \pi]$. Therefore, by (42) there are $(k' + 1)$ possible bifurcation values provided $f(m_1 e^2) < g(m_1 e^2) \in [2k'\pi + \pi/2, 2k'\pi + \pi]$. Since,

$$f(m_1 e^2) = 0 < 2k\pi + \pi = g(m_1 e^2) \quad \text{for each } k = 0, 1, 2, \dots,$$

there would be an infinite numbers of bifurcation values.

As before, we now should check the transversality condition, but since the argument is very similar to the previous case, so the analysis is omitted.

Summarizing the above, we have

Theorem 2.3 Suppose we treat L (i.e. the total loss rate of the immature) as a bifurcation parameter in equations (9)-(10). Assume that $\frac{p_1}{D_1^*} > e^2$ and r is sufficiently large so that there exist a positive integer k such that

$$r > \frac{\cos^{-1} \left((1 - \ln \frac{p_1}{D_1^*})^{-1} \right)}{\sqrt{(D_1^* (1 - \ln \frac{p_1}{D_1^*}))^2 - D_1^{*2}}},$$

where the range of $\cos^{-1}$ is taken to be $[2k\pi + \frac{\pi}{2}, 2k\pi + \pi]$. Let k' be the largest positive integer k that satisfies this condition. Then we will have $(k' + 1)$ bifurcation values $\hat{L}_i$, $i = 0, \dots, k'$. For L close to $\hat{L}_i$ the equilibrium E_1 undergoes a Hopf bifurcation in the w_1 direction. On the other hand, if $\frac{p_1}{D_1^*} \leq e^2$, Hopf bifurcation in the w_1 direction is not possible for E_1 .

Theorem 2.4 Suppose we treat p_2 as a bifurcation parameter in equations (9)-(10). Then,

- (i) if $\frac{p_1}{D_1^*} > e^2$ and r is sufficiently large so that there exist a positive integer k such that

$$r > \frac{\cos^{-1} \left((1 - \ln \frac{p_1 e^{-Lr}}{D_1^*})^{-1} \right)}{\sqrt{(D_1^* (1 - \ln \frac{p_1 e^{-Lr}}{D_1^*}))^2 - D_1^{*2}}},$$

where the range of $\cos^{-1}$ is taken to be $[2k\pi + \frac{\pi}{2}, 2k\pi + \pi]$. Let k' be the largest positive integer k that satisfies this condition. Then we will have $(k' + 1)$ bifurcation values $\hat{p}_{2i}$, $i = 0, \dots, k'$. For p_2 close to $\hat{p}_{2i}$ the equilibrium E_2 undergoes a Hopf bifurcation in the w_1 direction. On the other hand, if $\frac{p_1}{D_1^*} \leq e^2$, Hopf bifurcation in the w_1 direction on E_2 is not possible.

- (ii) there will be an infinite numbers of bifurcation values $\tilde{p}_{2i}$ ($i = 0, 1, \dots$) such that, for p_2 close to $\tilde{p}_{2i}$, the equilibrium E_2 undergoes a Hopf bifurcation in the w_2 direction.

2.5 Summary

In this section, we have looked at a two patch model for which individuals in patch 1 could not migrate to patch 2. We showed that this model can have two non-trivial equilibria E_1 and E_2 . We also looked at the stability conditions of these equilibria as

well as that of the trivial equilibrium when they all exist. We found that the trivial equilibrium E_0 and E_1 are always unstable and we provided the sufficient conditions for E_2 to be asymptotically stable. In the last part, we investigated the possibilities of Hopf bifurcation at E_1 and E_2 and showed that the existence of periodic solutions at these equilibria are possible.

3 Transcendental Equations

Since the stability analyses in Sections 4 and 5 will link to some rather difficult second order transcendental equations to solve. Therefore, we should have this section prior to them to discuss those transcendental equations.

3.1 Some Elementary Transcendental Equations

This section will be devoted to the solution of transcendental equations of the form

$$0 = N_0(z) + N_1(z)e^{-rz} + N_2(z)e^{-2rz}, \quad (43)$$

where $N_i(z)$, $i = 0, 1, 2$, is a polynomial of degree m_i such that $m_0 > m_1 > m_2$ and $r \geq 0$.

This type of equations often arises as characteristic equations in the study of stability of delay differential equations with constant delay. Since the stability of solutions of delay differential equations depends on the location of the zeros of their characteristic functions, we will emphasize on cases in which all roots have negative real parts [1][2]. In fact, more general transcendental equations had been studied by Pontrjagin [12]. The Theorems of Pontrjagin are listed in the Appendix A.

In this section, we will apply Pontrjagin's results to some special cases of (43). However, since these results are very general, it is usually quite difficult to apply Pontrjagin's Theorems. Therefore, our main goal is to translate his results into a more applicable one to our specific types of transcendental equations. That is, we will find necessary and sufficient conditions under which all their roots lie in the left half of the complex plane. In the first part, we will look at a second order case when $N_2(z) = 0$, which is exactly the type of transcendental equation we will encounter in Section 4. In the second part, we will look at a second order case when $N_2(z) \neq 0$, which is the type of transcendental equation we will see in Section 5. However, because of the complexity of the problem, we can only deal with it in a very restricted case.

3.2 A Second Order Case when $N_2(z) = 0$

A general second order case of (43) when $N_2(z) = 0$ is of the form

$$z^2 + Az + B + (Cz + D)e^{-rz} = 0, \quad (44)$$

where A, B, C , and D are real and r is a nonnegative constant .

General results as well as results in various special cases for equation (44) have been discussed in [10]. Some of the general results include: $z = 0$ is a root of (44) if and only if $B + D = 0$; and if $B + D < 0$ then there is a positive real root. There is also a positive real root if $B + D = 0$ and $A + C - rD < 0$. Finally if $A, B, C, D \geq 0$ and at least one of them is $\neq 0$, then there are no positive real roots.

Throughout this section we will investigate the roots of (44) with some restrictions on the parameters which corresponds to the characteristic equations which arise in Section 4. Namely, we assume $A > 0$ and $B \geq 0$. In fact, if we multiply (44) by $r^2 e^{zr}$ and let $\lambda = zr$, we get

$$(\lambda^2 + Ar\lambda + Br^2)e^\lambda + Cr\lambda + Dr^2. \quad (45)$$

Clearly, z is a root of (44) if and only if zr is a root of (45) provided that $r \neq 0$. When $r = 0$, (44) simply reduces to a quadratic equation, which can be easily solved. Therefore we shall assume that $r \neq 0$, and will consider solutions of equation of the following form

$$0 = (z^2 + Az + B)e^z + Cz + D, \quad (46)$$

where $A > 0$, $B \geq 0$, C , and D are real.

Before we proceed to prove any result, I want to mention that the methods we will develop depend heavily on Pontrjagin's results. So the reader should refer to appendix B for all the theorems that will be applied.

According to Theorem (B.3), we need to consider the following functions

$$\begin{aligned} h(z, t) &= (z^2 + Az + B)t + Cz + D \\ \text{and } H(z) &= h(z, e^z) = (z^2 + Az + B)e^z + Cz + D. \end{aligned} \quad (47)$$

By substituting, for real y , $z = iy$, we get

$$\begin{aligned} H(iy) &= F(y) + iG(y), \\ \text{where } F(y) &= (-y^2 + B) \cos y - Ay \sin y + D, \end{aligned} \quad (48)$$

$$G(y) = (-y^2 + B) \sin y + Ay \cos y + Cy. \quad (49)$$

Note that

$$G'(y) = (-y^2 + B) \cos y + A \cos y - (A + 2)y \sin y + C. \quad (50)$$

Clearly, the functions $F(y)$ and $G'(y)$ are even and $G(y)$ has $-y^2 \sin y$ as its principal term (consider having variables u and v in Definition B.2 replaced by $\cos y$ and $\sin y$, respectively).

Now, let us consider the roots of $G(y)$, or equivalently, the solution of

$$y^2 \sin y = (A \cos y + C)y + B \sin y. \quad (51)$$

First, we notice that both the left and right hand sides of (51) are odd functions. Furthermore $y = 0$ is a solution. Thus, we only need to consider $y > 0$. Observe the following for $y > 0$:

$$\sin y = 0 \quad \text{iff} \quad y = 2k\pi + \pi \text{ or } 2k\pi + 2\pi \quad \text{where } k = 0, 1, 2, \dots$$

If we substitute $y = 2k\pi + \pi$ in (51), we get

$$0 = (-A + C)(2k\pi + \pi).$$

This implies $y = 2k\pi + \pi$ is a solution of (51) if and only if $A = C$. Similarly, if we substitute $y = 2k\pi + 2\pi$ in (51), we get

$$0 = (A + C)(2k\pi + 2\pi),$$

which implies $y = 2k\pi + 2\pi$ is a solution of (51) if and only if $A = -C$.

Before we prove our first theorem, we need the following lemma.

Lemma 3.1 *Let*

$$g(y) \stackrel{\text{def}}{=} \frac{(A \cos y + C)y}{\sin y} + B,$$

where A, B, C are real and $B \geq 0$. Let $a > 0$ such that $\sin a \neq 0$. Then

$$a^2 \geq g(a) \implies (a + 2\pi)^2 > g(a + 2\pi).$$

Proof: Suppose

$$a^2 \geq g(a),$$

that is,

$$a^2 \geq \frac{(A \cos a + C)a}{\sin a} + B.$$

Then

$$a(a + 2\pi) \geq \frac{(A \cos a + C)(a + 2\pi)}{\sin a} + \frac{B(a + 2\pi)}{a},$$

so that

$$a(a + 2\pi) \geq \frac{(A \cos(a + 2\pi) + C)(a + 2\pi)}{\sin(a + 2\pi)} + B.$$

Thus,

$$(a + 2\pi)^2 > a(a + 2\pi) > g(a + 2\pi).$$

□

Theorem 3.1 *All the roots of $(z^2 + Az + B)e^z + Cz + D$, where $A > |C|$ and $B \geq 0$, have negative real parts if and only if at each of the finite number of roots of $G(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, we have $G'(y)F(y) > 0$.*

Proof: Since $A > |C|$, y cannot be a solution of (51) if $\sin y = 0$. Therefore, we can consider the solution of the following equation instead

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B. \quad (52)$$

Note that the functions on both sides of (52) are even. Let

$$g(y) = \frac{(A \cos y + C)y}{\sin y} + B.$$

Then we have,

$$\begin{aligned} \lim_{y \rightarrow 0^+} g(y) &= A + B + C > 0, \\ \lim_{y \rightarrow (2k\pi + \pi)^-} g(y) &= -\infty, \\ \lim_{y \rightarrow (2k\pi + \pi)^+} g(y) &= +\infty, \\ \lim_{y \rightarrow (2k\pi + 2\pi)^-} g(y) &= -\infty, \\ \lim_{y \rightarrow (2k\pi + 2\pi)^+} g(y) &= +\infty. \end{aligned}$$

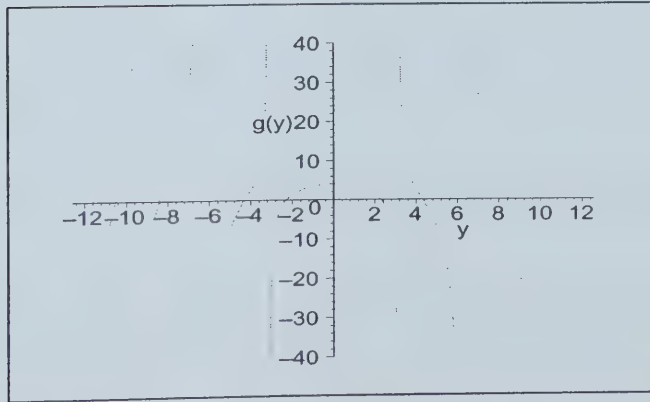


Figure 1: $A > |C|$: The graph of $g(y)$ with $A = 2$, $B = 1$, and $C = 1$.

It is easy to see that the function y^2 intersects $g(y)$ at least twice in each of the intervals $[2k\pi, 2k\pi + 2\pi]$, where $k = 0, 1, 2, \dots$.

Since $-y^2 \sin y$ is the principal term of $G(y)$, we may choose ε in Theorem B.2 to be any real number as long as $\sin \varepsilon \neq 0$. In particular, we choose ε so that $A \cos \varepsilon + C = 0$, $\varepsilon \in (0, \pi)$. Thus, if we choose k big enough such that $(2k\pi - \varepsilon)^2 > B$, then $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ contains exactly $2(2)k+1+1$ real solutions of (52) (including the root 0 and because the most negative root is actually on $(-2k\pi + \varepsilon, -2k\pi + \pi)$ and the most positive root is on $(2k\pi, 2k\pi + \varepsilon)$). Therefore, $G(y)$ has $4k+2$ real roots for k sufficiently large. This shows that all roots of $G(y)$ are real by Theorem B.2.

Next, we will consider the sign of $G'(y)F(y)$ for the roots of $G(y)$. The simplest one to consider is the root $y = 0$, we have

$$G'(0)F(0) = (A + B + C)(B + D). \quad (53)$$

Since $(A + B + C) > 0$, we need $(B + D) > 0$. Now, we consider all the positive real roots of $G(y)$. For convenience, we shall label all the nonnegative roots. Set $a_0 = 0$. Let a_{2k+1} be the sole root of $G(y)$ on $(2k\pi, 2k\pi + \pi)$, and a_{2k+2} be the sole root of $G(y)$ on $(2k\pi + \pi, 2k\pi + 2\pi)$, where $k = 0, 1, 2, \dots$. For all the positive roots a , by (52), we have

$$(a^2 - B) \sin a = (A \cos a + C)a. \quad (54)$$

Multiplying (50) by $(a^2 - B)$ and substituting (54), we get

$$\begin{aligned} (a^2 - B)G'(a) &= -[a^4 + (A^2 + A - 2B)a^2 + B(A + B)] \cos a \\ &\quad - [(A + 1)Ca^2 + CB] \\ \text{or} \quad (a^2 - B)G'(a) &= -[P_1(a) \cos a + Q_1(a)], \end{aligned} \quad (55)$$

where $P_1(a) = a^4 + (A^2 + A - 2B)a^2 + B(A + B)$ and $Q_1(a) = (A + 1)Ca^2 + CB$. We see that $P_1(a)$ is a polynomial of degree 4 with positive coefficient of the highest order term and $Q_1(a)$ is a polynomial of degree 2. Similarly, if we multiply (48) by $(a^2 - B)$ and substituting (54), we get

$$\begin{aligned} (a^2 - B)F(a) &= -[a^4 + (A^2 - 2B)a^2 + B^2] \cos a - [(AC - D)a^2 + BD] \\ \text{or} \quad (a^2 - B)F(a) &= -[P_2(a) \cos a + Q_2(a)], \end{aligned} \quad (56)$$

where $P_2(a) = a^4 + (A^2 - 2B)a^2 + B^2$ and $Q_2(a) = (AC - D)a^2 + BD$. Then $P_2(a)$ is a polynomial of degree 4 with positive coefficient of the highest order term and $Q_2(a)$ is a polynomial of degree 2. Thus,

$$(a^2 - B)^2 G'(a)F(a) = [P_1(a) \cos a + Q_1(a)][P_2(a) \cos a + Q_2(a)]. \quad (57)$$

To finish our proof, we consider the following:

For $a = a_{2k+1}$, $k = 0, 1, 2, \dots$, we have $a_{2k+1} + 2\pi > a_{2(k+1)+1}$ by Lemma 3.1. This implies $\cos(a_{2k+1})$ is an increasing sequence. In fact, it increases up to the limit 1,

because for any positive real number a such that $\sin a \neq 0$, if k is sufficiently large, we must have

$$(a+2k\pi)^2 > \frac{(A \cos a + C)(a + 2k\pi)}{\sin a} + B \iff (a+2k\pi) > \frac{(A \cos a + C)}{\sin a} + \frac{B}{(a + 2k\pi)}.$$

Therefore, $G'(a_{2k+1})F(a_{2k+1}) > 0$ when k is sufficiently large (i.e. there exists a number $m_1 > 0$ such that $G'(a_{2k+1})F(a_{2k+1}) > 0$ whenever $a_{2k+1} > m_1$).

For $a = a_{2k+2}$, $k = 0, 1, 2, \dots$, similarly, we have $a_{2k+2} + 2\pi > a_{2(k+1)+2}$ by Lemma 3.1. This implies $\cos(a_{2k+2})$ is an decreasing sequence. In fact, it decreases down to the limit -1 by the same argument as above.

Therefore, $G'(a_{2k+2})F(a_{2k+2}) > 0$ when k is sufficiently large (i.e. there exists a number $m_2 > 0$ such that $G'(a_{2k+2})F(a_{2k+2}) > 0$ whenever $a_{2k+1} > m_2$).

Finally, we choose $m = \max\{m_1, m_2\}$. Then, by applying Theorem B.3, the Theorem is proved. □

In the following, not only that I will explain how such an m in Theorem 3.1 can be found, I am going to give it out as an algorithm to determine whether a given transcendental equation, which fits the hypothesis of Theorem 3.1, has all its roots lie in the left half plane. The idea is easy, so detailed explanations are not given.

Procedure

(Step 1) (Check $G'(0)F(0) > 0$)

Check $B + D > 0$.

(Step 2)

Choose k' big enough such that the sole root of $G(y)$ in $(2k'\pi, 2k'+\pi)$, call it a_{odd} , has $\cos(a_{odd}) > 0$ and the sole root of $G(y)$ in $(2k'\pi + \pi, 2k' + 2\pi)$, call it a_{even} , has $\cos(a_{even}) < 0$.

(Step 3) (The idea is to find the interval (m, ∞) such that for all the roots $a_{2k+1} \in (m, \infty)$, the condition $G'(a_{2k+1})F(a_{2k+1}) > 0$ is guaranteed. Note that a_{2k+1} comes from the proof of Theorem 3.1.)

Let $\alpha = \cos(a_{\text{odd}}) > 0$.

Let $M_1(w, y) = wP_1(y) + Q_1(y)$, w is real.

Choose m_1 large enough so that for each $y > m_1$ and $w \geq \alpha$, we have $M_1(w, y) > 0$. It can be found as follows.

Since,

$$P_1(y) = \left(y^2 + \frac{A^2 + A - 2B}{2}\right)^2 - \left[\frac{(A^2 + A - 2B)^2}{4} - B(A + B)\right] \quad \text{and}$$

$$Q_1(y) = (A + 1)Cy^2 + CB.$$

Case 1) $(A + 1)C \geq 0$.

Pick $m_1^2 > \sqrt{K_2} - K_1$,

where $K_1 = \frac{A^2 + A - 2B}{2}$, $K_2 = \frac{(A^2 + A - 2B)^2}{4} - B(A + B)$.

Since $\sqrt{K_2} - K_1$ is always ≤ 0 , we can pick $m_1 = 0$.

Case 2) $(A + 1)C < 0$.

Since,

$$\begin{aligned} M_1(\alpha, y) &= \alpha P_1(y) + Q_1(y) \\ &= \alpha(y^4 + K_1 y^2 + K_2) \\ &= \alpha \left[\left(y^2 + \frac{K_1}{2}\right)^2 - \frac{K_1^2}{4} + K_2 \right]. \end{aligned}$$

We pick $m_1^2 > \sqrt{\frac{K_1^2}{4} - K_2} - \frac{K_1}{2}$,

where $K_1 = \frac{(A + 1)C}{\alpha} + (A^2 + A - 2B)$, $K_2 = \frac{CB}{\alpha} + B(A + B)$.

Similarly, let $M_2(w, y) = wP_2(y) + Q_2(y)$, w is real. Choose m_2 big enough such that for each $y > m_2$ and $w \geq \alpha$, we have $M_2(w, y) > 0$. It can be found as follows.

Since,

$$P_2(y) = (y^2 + \frac{A^2 - 2B}{2})^2 - \left[\frac{(A^2 - 2B)^2}{4} - B^2 \right] \quad \text{and}$$

$$Q_2(y) = (AC - D)y^2 + BD.$$

Case 1) $AC - D > 0$.

$$\text{Pick} \quad m_2^2 > \max \left\{ \sqrt{K_2} - K_1, \frac{-BD}{AC - D} \right\},$$

$$\text{where} \quad K_1 = \frac{A^2 - 2B}{2}, \quad K_2 = \frac{(A^2 - 2B)^2}{4} - B^2.$$

$$\text{Since } \sqrt{K_2} - K_1 \text{ is always } \leq 0, \text{ we pick } m_2^2 > \frac{-BD}{AC - D}.$$

Case 2) $AC - D = 0$.

When $BD \geq 0$,

$$\text{pick} \quad m_2 = 0;$$

when $BD < 0$,

$$\text{pick} \quad m_2^2 > \sqrt{K_2 - BD} - K_1,$$

where K_1 and K_2 are defined exactly as in **Case 1** right above.

Case 3) $AC - D < 0$.

Since,

$$\begin{aligned} M_2(\alpha, y) &= \alpha P_2(y) + Q_2(y) \\ &= \alpha \left[(y^2 + \frac{K_1}{2})^2 - \frac{K_1^2}{4} + K_2 \right]. \end{aligned}$$

$$\text{We pick} \quad m_2^2 > \max \left\{ \sqrt{\frac{K_1^2}{4} - K_2} - \frac{K_1}{2}, \frac{-BD}{AC - D} \right\},$$

$$\text{where} \quad K_1 = \frac{AC - D}{\alpha} + (A^2 - 2B), \quad K_2 = \frac{BD}{\alpha} + B^2.$$

Finally, let $m = \max\{m_1, m_2\}$, and pick k'' an integer so that $m \leq 2k''\pi$. Choose $\bar{k} = \max\{k', k''\}$. Then, check the conditions $G'(y)F(y) > 0$ for each of the sole root of $G(y)$, $y \in (2k\pi, 2k\pi + \pi)$, $k = 0, 1, 2, \dots, \bar{k} - 1$.

(Step 4)(The idea is the same as **Step 3**, but we now work on a_{2k+2} instead)

Let $\beta = \cos(a_{\text{even}}) < 0$.

Let $M_1(w, y) = wP_1(y) + Q_1(y)$, w is real.

Choose m_1 large enough so that for each $y > m_1$ and $w \leq \beta$, we have $M_1(w, y) < 0$. It can be found as follow.

Case 1) $(A + 1)C \leq 0$.

Pick $m_1^2 > \sqrt{K_2} - K_1$,

where $K_1 = \frac{A^2 + A - 2B}{2}$, $K_2 = \frac{(A^2 + A - 2B)^2}{4} - B(A + B)$.

Since $\sqrt{K_2} - K_1$ is always ≤ 0 , we can pick $m_1 = 0$.

Case 2) $(A + 1)C > 0$.

Pick $m_1^2 > \sqrt{\frac{K_1^2}{4} - K_2} - \frac{K_1}{2}$,

where $K_1 = \frac{(A + 1)C}{\beta} + (A^2 + A - 2B)$, $K_2 = \frac{CB}{\beta} + B(A + B)$.

Similarly, let $M_2(w, y) = wP_2(y) + Q_2(y)$, w is real. Choose m_2 large enough such that for each $y > m_2$ and $w \leq \beta$, we have $M_2(w, y) < 0$. It can be found as follow.

Case 1) $AC - D < 0$.

Pick $m_2^2 > \max \left\{ \sqrt{K_2} - K_1, \frac{-BD}{AC - D} \right\}$,

where $K_1 = \frac{A^2 - 2B}{2}$, $K_2 = \frac{(A^2 - 2B)^2}{4} - B^2$.

Since $\sqrt{K_2} - K_1$ is always ≤ 0 , we pick $m_2^2 > \frac{-BD}{AC - D}$.

Case 2) $AC - D = 0$.

When $BD < 0$, pick $m_2 = 0$;
 when $BD \geq 0$, pick $m_2^2 > \sqrt{K_2 - BD} - K_1$,

where K_1 and K_2 are defined exactly as in **Case 1** above.

Case 3) $AC - D > 0$.

Pick $m_2^2 > \max \left\{ \sqrt{\frac{K_1^2}{4} - K_2} - \frac{K_1}{2}, \frac{-BD}{AC - D} \right\}$,

where $K_1 = \frac{AC - D}{\beta} + (A^2 - 2B)$, $K_2 = \frac{BD}{\beta} + B^2$.

Finally, let $m = \max\{m_1, m_2\}$, and pick k'' an integer so that $m \leq 2k''\pi$.
 Choose $\bar{k} = \max\{k', k''\}$. Then, check the conditions $G'(y)F(y) > 0$ for
 each of the sole root $y \in (2k\pi + \pi, 2k\pi + 2\pi)$, $k = 0, 1, 2, \dots, \bar{k} - 1$.

End of Procedure

Remarks:

- Any term with an undefined $\sqrt{}$ should be replaced by 0 (e.g. if $K_2 - BD < 0$ then the whole term $\sqrt{K_2 - BD} - K_1$ should be replaced by 0).
- Sometimes it is preferable to pick a slightly bigger k' in **Step 2**, since then $\cos(a_{odd})$ and $\cos(a_{even})$ would be closer to 1 and -1, respectively, which in turn could produce smaller $\bar{k}$'s in **Step 3** and **Step 4**.

Similarly, we can establish theorems like Theorem 3.1 for $0 \leq A < |C|$, $A = C$, and $A = -C$. Since the technique in proving these theorems is very similar to the one we used to prove Theorem 3.1, only the parts which are essentially different from the proof of Theorem 3.1 are given in detail. First, we need the following lemmas.

Lemma 3.2 (i) If $C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $I_k := (2k\pi, 2k\pi + \pi)$ contains at most two real roots of $G(y)$. (ii) if $-C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $J_k := (2k\pi + \pi, 2k\pi + 2\pi)$ contains at most two real roots of $G(y)$.

Proof: Consider the case $C > A \geq 0$ and $B \geq 0$. Instead of looking at the roots of $G(y)$ in the intervals I_k , $k = 0, 1, 2, \dots$, equivalently, we look at the solutions of the equation

$$y = \frac{(A \cos y + C)}{\sin y} + \frac{B}{y}.$$

Let

$$h(y) = \frac{(A \cos y + C)}{\sin y} + \frac{B}{y},$$

then

$$h'(y) = - \left[\frac{A + C \cos y}{\sin^2(y)} + \frac{B}{y^2} \right].$$

Clearly, $h'(y) \geq 0$ implies $\cos y < 0$ (i.e. $y > 2k\pi + \pi/2$, $y \in I_k$). In fact, it is easy to see that $h'(y)$ is increasing in the set $\{y \in I_k | h'(y) \geq 0\}$, which is an interval. Thus, it is not possible to have the function $f(y) = y$, which has constant positive slope, intersect $h(y)$ more than twice.

A similar argument works for the case $-C > A \geq 0$ and $B \geq 0$. □

Lemma 3.3 (i) If $C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $I_k := (2k\pi + \pi, 2k\pi + 2\pi)$ contains at most two real roots of $G(y)$. (ii) If $-C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $J_k := (2k\pi, 2k\pi + \pi)$ contains at most two real roots of $G(y)$.

Proof: Suppose $C > A \geq 0$ and $B \geq 0$, again we will look at the solution of

$$y = \frac{(A \cos y + C)}{\sin y} + \frac{B}{y}.$$

Let

$$h(y) = \frac{(A \cos y + C)}{\sin y} + \frac{B}{y}.$$

Then

$$h'(y) = - \left[\frac{A + C \cos y}{\sin^2(y)} + \frac{B}{y^2} \right]$$

and

$$h''(y) = \frac{C}{\sin y} + \frac{2 \cos y (A + C \cos y)}{\sin^3(y)} + \frac{2B}{y^3}.$$

Observation: $h'(y) < 0$ when $2k\pi + 3\pi/2 \leq y \in I_k$.

All we need to show is that $h''(y) < 0$ when $h'(y) \geq 0$, $y \in I_k$. First, we see that

$$h'(y) \geq 0 \iff \frac{A + C \cos y}{\sin^2(y)} + \frac{B}{y^2} \leq 0. \quad (58)$$

Now, suppose $h'(y) \geq 0$. By (58), we have

$$\begin{aligned} h''(y) &\leq \frac{C}{\sin y} - \frac{2 \cos y}{\sin y} \frac{B}{y^2} + \frac{2B}{y^3} \\ &= \frac{C}{\sin y} + \frac{2B}{y^2} \left(\frac{1}{y} - \frac{1}{\tan y} \right). \end{aligned}$$

Note that, if $B = 0$ then we are done. Otherwise, there are two intervals Y_1 and Y_2 such that $Y_1 \cup Y_2 = (2k\pi + \pi, 2k\pi + 3\pi/2)$ and $y > \tan y$ for each $y \in Y_1$ and $y \leq \tan y$ for each $y \in Y_2$. Thus, when $y \in Y_1$, we certainly have $h''(y) < 0$. On the other hand, when $y \in Y_2$, we consider the following:

Inequality (58) implies

$$\begin{aligned} \frac{C \cos y}{\sin^2 y} = \frac{C}{\sin y \tan y} &\leq -\frac{B}{y^2} < -\frac{2B}{y^3}, \quad \text{since } y > 2. \\ \implies \frac{C}{\sin y} &< -\frac{2B \tan y}{y^2 y}. \end{aligned} \quad (59)$$

Then, since

$$\frac{C}{\sin y} + \frac{2B}{y^2} \left(\frac{1}{y} - \frac{1}{\tan y} \right) < \frac{C}{\sin y} + \frac{2B \tan y}{y^2 y},$$

we have $h''(y) < 0$ by (59).

A similar argument works for the case $-C > A \geq 0$ and $B \geq 0$, except the interval $J_0 = (0, \pi)$. This is because argument like inequality (59) may not be valid

anymore. Thus, it has to be treated differently. For $y \in J_0$, we look at the solutions of the following equation instead

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B.$$

Let

$$g(y) = \frac{(A \cos y + C)y}{\sin y} + B.$$

Then

$$g'(y) = -Ay + \frac{A \cos y + C}{\sin^2 y}(\sin y - y \cos y).$$

Since $-C > A > 0$, we can see that $\frac{A \cos y + C}{\sin^2 y} < 0$. Also, because the function $f(y) = \sin y - y \cos y$ has no real root in J_0 (consider the solution of $y = \tan y$ in J_0) and $f(\pi/2) > 0$, we can conclude that $g(y)$ is always decreasing in J_0 . So, clearly, $G(y)$ has no more than one root in J_0 . □

Lemma 3.4 (i) If $C > A \geq 0$ and $B \geq 0$, then if $k' \geq 0$ is an integer such that $(2k'\pi, 2k'\pi + \pi)$ contains a root of $G(y)$ then for any integer $k \geq k'$ the interval $I_k := (2k\pi + \pi, 2k\pi + 2\pi)$ contains no real root of $G(y)$. (ii) If $-C > A \geq 0$ and $B \geq 0$, then if $k' \geq 0$ is an integer such that $(2k'\pi + \pi, 2k'\pi + 2\pi)$ contains a root of $G(y)$ then for any integer $k > k'$ the interval $J_k := (2k\pi, 2k\pi + \pi)$ contains no real root of $G(y)$.

Proof: Suppose $C > A \geq 0$ and $B \geq 0$, we look at the solution of

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B$$

in the interval I_k . Call the right hand side $g(y)$. First, we see that since $\frac{(A \cos y + C)y}{\sin y} < 0$ in I_k , we have $g(y) < B$ in I_k . Also, because $G(y)$ has a root in $(2k'\pi, 2k'\pi + \pi)$, there exist a number $a \in (2k'\pi, 2k'\pi + \pi)$ such that $a^2 = g(a) > B$ (since $\frac{(A \cos y + C)y}{\sin y} > 0$ in $(2k'\pi, 2k'\pi + \pi)$). Hence (i) is proved.

Similar argument works for the case $-C > A \geq 0$ and $B \geq 0$. □

Lemma 3.5 (i) If $C > A \geq 0$ and $B \geq 0$, then for k sufficiently large, the interval $I_k := (2k\pi, 2k\pi + \pi)$ contains exactly two distinct real roots of $G(y)$. (ii) if $-C > A \geq 0$ and $B \geq 0$, then for k sufficiently large, the interval $J_k := (2k\pi + \pi, 2k\pi + 2\pi)$ contains exactly two distinct real roots of $G(y)$.

Proof: Suppose $C > A \geq 0$ and $B \geq 0$. Again we look at the solution of

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B$$

in the interval I_k . Call the right hand side $g(y)$. It is easy to show that

$$\lim_{y \rightarrow (2k\pi)^+} g(y) = \infty$$

and

$$\lim_{y \rightarrow (2k\pi + \pi)^-} g(y) = \infty,$$

for $k > 0$. Also, for k sufficiently large, we have

$$(2k\pi + \pi/2)^2 > g(2k\pi + \pi/2) = C(2k\pi + \pi/2) + B.$$

Therefore, we have exactly 2 distinct real roots of $G(y)$ for sufficiently large k by Lemma 3.1 and Lemma 3.2.

Similar argument works for the case $-C > A \geq 0$ and $B \geq 0$.

□

Summarizing all the lemmas above, we get:

1. If $C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $I_k = (k\pi, k\pi + \pi)$ contains at most two real roots of $G(y)$. In particular, for k sufficiently large, I_k contains no real root, if k is *odd*, and I_k contains exactly 2 distinct real roots, if k is *even*.
2. If $-C > A \geq 0$ and $B \geq 0$, then for $k = 0, 1, 2, \dots$, each of the intervals $I_k = (k\pi, k\pi + \pi)$ contains at most two real roots of $G(y)$. In particular, the interval $I_0 = (0, \pi)$ contains at most one root. And, for k sufficiently large, I_k contains no real root, if k is *even*, and I_k contains exactly 2 distinct real roots, if k is *odd*.

For all of the following Theorems, I will not show explicitly how the interval $[0, m]$ is found as I did for Theorem 3.1. Since the analysis is straightforward, the reader can refer to the **Procedure** on page 25 for an example.

Theorem 3.2 *All the roots of $(z^2 + Az + B)e^z + Cz + D$, where $C > A \geq 0$ and $B \geq 0$, have negative real parts iff it satisfies the following conditions*

- (i) $k \geq 0$ is the first integer such that the interval $(2k\pi, 2k\pi + \pi)$ contains 2 distinct real roots implies $k = 0$ or the interval $(2k\pi - \pi, 2k\pi)$ contains 2 distinct real roots as well; and
- (ii) at each of the finite number of roots of $G(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, we have $G'(y)F(y) > 0$.

Proof: Since $C > A \geq 0$, y cannot be a root of $G(y)$ if $\sin y = 0$. We consider the solution of the following equation instead

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B. \quad (60)$$

Let

$$g(y) = \frac{(A \cos y + C)y}{\sin y} + B.$$

Then we have,

$$\lim_{y \rightarrow 0^+} g(y) = A + B + C, \quad (61)$$

$$\lim_{y \rightarrow (2k\pi + \pi)^-} g(y) = +\infty, \quad (62)$$

$$\lim_{y \rightarrow (2k\pi + \pi)^+} g(y) = -\infty, \quad (63)$$

$$\lim_{y \rightarrow (2k\pi + 2\pi)^-} g(y) = -\infty, \quad (64)$$

$$\lim_{y \rightarrow (2k\pi + 2\pi)^+} g(y) = +\infty. \quad (65)$$

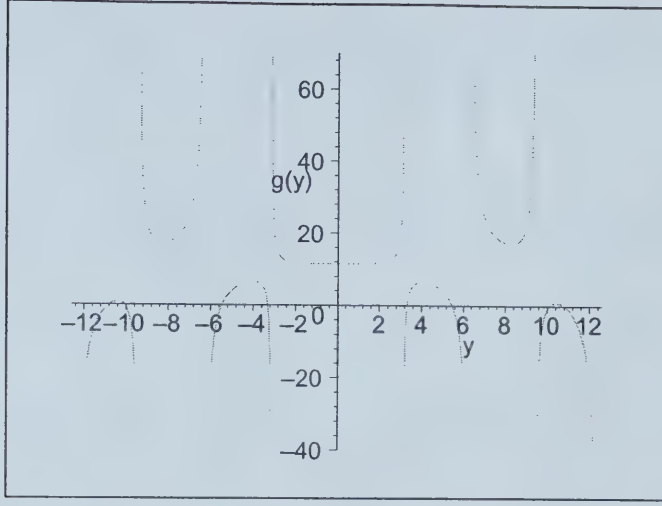


Figure 2: $C > A \geq 0$: The graph of $g(y)$ when $A = 1$, $B = 2$, and $C = 10$.

First, since $-y^2 \sin y$ is the principal term of $G(y)$, we may choose ε in Theorem B.2 to be $\pi/2$. Now, by Lemma 3.5, we know that there are exactly 2 distinct real roots contained in $I_k = (2k\pi, 2k\pi + \pi)$ for k sufficiently large. Let k' be the first integer that is big enough. For convenience, we name the smaller and the larger root in $I_{k'}$ by a_1 and a_2 , respectively. Similarly, the smaller root in $I_{k'+1}$ is named a_3 and the larger root in $I_{k'+1}$ is named a_4 , and so on. Then, by Lemma 3.1 and (62)–(65), $\cos(a_{2k+1})$, $k = 0, 1, 2, \dots$ is an increasing sequence which increases up to 1 and $\cos(a_{2k+2})$, $k = 0, 1, 2, \dots$ is a decreasing sequence which decreases down to -1.

So, one should be able to see that when k is sufficiently large, $G(y)$ has exactly $2(2)k + 1 + 1$ roots (one of the 1's comes from the root 0 and the other 1 comes from the root in the interval $(2k\pi, 2k\pi + \varepsilon)$) in the interval $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ **iff** each of the intervals $(2k\pi, 2k\pi + 2\pi)$, $k = 0, 1, 2, \dots$ has exactly 2 distinct real roots. By the previous summary and by Lemma 3.4, we can conclude that each of the intervals $(2k\pi, 2k\pi + 2\pi)$, $k = 0, 1, 2, \dots$ has exactly 2 distinct real roots **iff** $k \geq 0$ is the first integer such that the interval $(2k\pi, 2k\pi + \pi)$ contains 2 distinct real roots implies $k = 0$ or the interval $(2k\pi - \pi, 2k\pi)$ contains 2 distinct real roots as well.

The next step will be to look at $G'(y)F(y)$ for all the roots of $G(y)$, and clearly, the argument will be the same as the one in Theorem 3.1. □

Theorem 3.3 *All the roots of $(z^2 + Az + B)e^z + Cz + D$, where $-C > A \geq 0$ and $B \geq 0$, have negative real parts iff it satisfies the following conditions*

- (i) $A + B + C > 0$;
- (ii) $k \geq 0$ is the first integer such that the interval $(2k\pi + \pi, 2k\pi + 2\pi)$ contains 2 distinct real roots implies $k = 0$ or the interval $(2k\pi, 2k\pi + \pi)$ contains 2 distinct real roots as well; and
- (iii) at each of the finite number of roots of $G(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, we have $G'(y)F(y) > 0$.

Proof: The proof is almost exactly the same as the proof of Theorem 3.2, so I would not repeat it. However, I would like to point out how the condition $A + B + C > 0$ come about. In fact, this condition is needed when we try to show that there are $4k + 2$ real roots in the interval $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ for sufficiently large k . Since I would not go into the details, I choose an easier way to explain it. Recall that

$$G'(0)F(0) = (A + B + C)(B + D).$$

Since, we need it to be positive, therefore $(A + B + C)$ must not be 0. Also, by the general results mentioned in page 21, $(B + D)$ has to be > 0 . This implies $(A + B + C)$ must be > 0 . One may notice, the condition $A + B + C > 0$ can be replaced by $B + D > 0$.

□

Theorem 3.4 *All the roots of $(z^2 + Az + B)e^z + Cz + D$, where $A = C > 0$ and $B \geq 0$, have negative real parts if and only if at each of the finite number of roots of $G(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, we have $G'(y)F(y) > 0$.*

Proof: Since $A = C$, we know that $2k\pi + \pi$, $k = 0, 1, 2, \dots$ must be roots of $G(y)$. For the rest of the roots, we consider the solution of the following equation

$$y^2 = \frac{(A \cos y + C)y}{\sin y} + B. \quad (66)$$

Let

$$g(y) = \frac{(A \cos y + C)y}{\sin y} + B.$$

Then it is easy to show that,

$$\lim_{y \rightarrow 0^+} g(y) = A + B + C > 0, \quad (67)$$

$$\lim_{y \rightarrow (2k\pi + \pi)} g(y) = B, \quad (68)$$

$$\lim_{y \rightarrow (2k\pi + 2\pi)^-} g(y) = -\infty, \quad (69)$$

$$\lim_{y \rightarrow (2k\pi + 2\pi)^+} g(y) = +\infty. \quad (70)$$

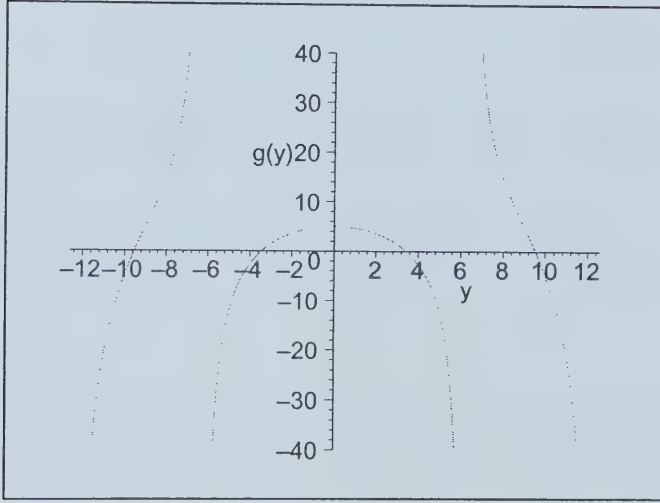


Figure 3: $A = C > 0$: The graph of $g(y)$ when $A = 2, B = 1$, and $C = 2$.

First, we look at $G'(y)F(y)$ for the root 0 and the roots $y_k = 2k\pi + \pi$, $k = 0, 1, 2, \dots$ since $G'(0)F(0) = (A + B + C)(B + D)$, we can conclude that $A + B + C$ has to be > 0 as explained in the proof of Theorem 3.3, but this is obviously true. For the roots $y_k = 2k\pi + \pi$, $k = 0, 1, 2, \dots$, we have

$$G'(y_k)F(y_k) = (y_k^2 - B)(y_k^2 - B + D), \quad (71)$$

obviously, we cannot allow $y_k^2 = B$ for any $k = 0, 1, 2, \dots$ and for sufficiently large k , we must have $G'(y_k)F(y_k) > 0$ (i.e. there exists a number $m_1 > 0$ such that $G'(y_k)F(y_k) > 0$ whenever $y_k > m_1$).

Now, we shall assume $y_k^2 = (2k\pi + \pi)^2 \neq B$ for any $k = 0, 1, 2, \dots$. Then, we may choose ε in Theorem B.2 to be $\pi/2$. Since y^2 intersects $g(y)$ at least once in every interval $(2k\pi, 2k\pi + 2\pi)$, $k = 0, 1, 2, \dots$, and never at $y_k = 2k\pi + \pi$. Thus, by lemma 3.1 and (67)–(70), for sufficiently large k , $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ must contain exactly

$2(2)k + 1 + 1$ real roots of $G(y)$. This proves that all roots of $G(y)$ are real.

For convenience, we name the sole root $\neq 2k\pi + \pi$ in $(2k\pi, 2k\pi + 2\pi)$ to be a_k , then by lemma 3.1 and (67)–(70), we must have $\cos(a_k)$, $k = 0, 1, 2, \dots$ to be an increasing sequence for big enough k (i.e. $a_k^2 > B + |D|$), in fact, it increases up to 1. Similarly, as in the proof of Theorem 3.1, we can conclude that for sufficiently large k , we must have $G'(a_k)F(a_k) > 0$ (i.e. there exists a number $m_2 > 0$ such that $G'(a_k)F(a_k) > 0$ whenever $a_k > m_2$).

Finally, pick $m = \max\{m_1, m_2\}$.

□

The following Theorem is stated without proof, since the analysis is analogous to the previous case.

Theorem 3.5 *All the roots of $(z^2 + Az + B)e^z + Cz + D$, where $A = -C > 0$ and $B \geq 0$, have negative real parts iff it satisfies the following conditions*

- (i) $B > 0$; and
- (ii) *at each of the finite number of roots of $G(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, we have $G'(y)F(y) > 0$.*

As we can see, Theorem 3.1–3.5 have provided a way to determine whether all roots of (44) with $A > 0$ and $B \geq 0$ have negative real parts. This is exactly the type of equations that we will be dealing with in Section 4.

3.3 A Second Order Case when $N_2(z) \neq 0$

A general second order case of (43) when $N_2(z) \neq 0$ is of the form

$$z^2 + Az + B + (C + Dz)e^{-rz} + Ee^{-2rz} = 0, \quad (72)$$

where A, B, C, D , and E are real and r is a nonnegative constant.

Similarly, if we multiply (72) by $r^2 e^{2rz}$ and set $\lambda = rz$, we get

$$(\lambda^2 + Ar\lambda + Br^2)e^{2\lambda} + (Cr^2 + Dr\lambda)e^\lambda + Er^2. \quad (73)$$

Therefore, we should look at solution of equations of the form

$$0 = (z^2 + Az + B)e^{2z} + Ce^z + Dze^z + E, \quad (74)$$

where A, B, C, D , and E are real.

In fact, the transcendental equation that we will see in section 5 has $A, B > 0$. However, because of the difficulty of the problem, we will only study a special case where all the parameters are positive and with $A > C$ and $A > D$. Now, we do similar analysis on equation (74) as we did in section 3.2. However, since the analysis is analogous to those in section 3.2, only an outline is given here.

Let the function $H(z)$ be the right hand side of (74). Then, substitute $z = iy$ and get

$$\begin{aligned} H(iy) &= (-y^2 + Aiy + B)e^{i2y} - (iDy + C)e^{iy} + E \\ &= F(y) + iG(y), \end{aligned}$$

where

$$\begin{aligned} F(y) &= (-y^2 + B) \cos 2y - Ay \sin 2y - C \cos y + Dy \sin y + E, \\ G(y) &= (-y^2 + B) \sin 2y + Ay \cos 2y - C \sin y - Dy \cos y. \end{aligned}$$

As before we need to show that $G(y) = 0$ has simple real roots only. First we notice that 0 is certainly a root, and because of the assumptions $A > C$ and $A > D$, one can show that y cannot be a root if $\sin 2y = 0$, except $y = 0$. Then, we will look at the equation

$$y^2 = \frac{(A \cos 2y - D \cos y)y}{\sin 2y} - \frac{C}{2 \cos y} + B.$$

Thus, if we let $g(y)$ be the right hand side of this equation, we can see

$$\begin{aligned}
\lim_{y \rightarrow 0} g(y) &= \frac{1}{2}(A - C - D + 2B), \\
\lim_{y \rightarrow 2k\pi + \pi/2^-} g(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + \pi/2^+} g(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + \pi^-} g(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + \pi^+} g(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + 3\pi/2^-} g(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + 3\pi/2^+} g(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + 2\pi^-} g(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + 2\pi^+} g(y) &= \infty.
\end{aligned}$$

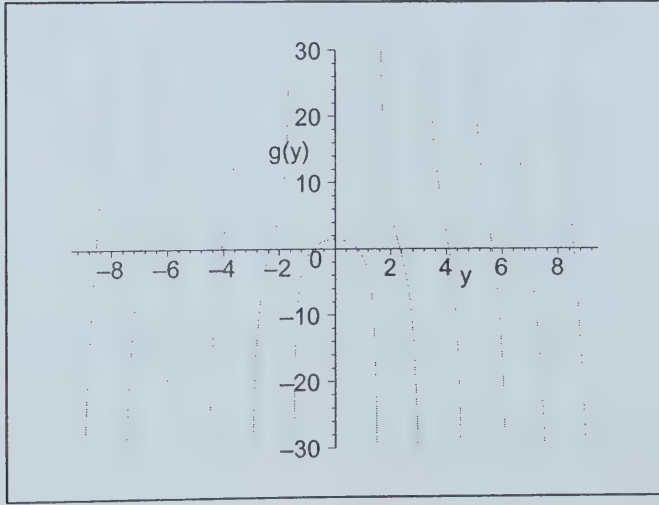


Figure 4: $A > C, D$: The graph of $g(y)$ with $A = 3, B = 1, C = 1$, and $D = 1$.

It is easy to see that if $(A - C - D + 2B) > 0$, $(y^2$ will intersect $g(y)$ at least 4 times in each of these intervals $[2k\pi, 2k\pi + 2\pi]$, where $k = 0, 1, 2, \dots$

Since, the principle terms of $G(y)$ is $-y^2 \sin 2y$, we may choose ε to be any real number as long as $\sin 2\varepsilon \neq 0$. Then, easily, one can show that $G(y)$ has exactly $8k + 2$ real roots in $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ for k sufficiently large. This shows that all roots of $G(y)$ are real when $(A - C - D + 2B) > 0$. On the other hand, if

$(A - C - D + 2B) \leq 0$, one should see that it is not possible for $G(y)$ to have $8k+2$ real roots in $(-2k\pi + \varepsilon, 2k\pi + \varepsilon)$ for any k . For a more rigorous argument, one should consider the number of possible real solution in each of these intervals $(2k\pi, 2k\pi + \pi/2)$, $(2k\pi + \pi/2, 2k\pi + \pi)$, $(2k\pi + \pi, 2k\pi + 3\pi/2)$, and $(2k\pi + 3\pi/2, 2k\pi + 2\pi)$, in fact, there cannot be more than 1. This can be done by assuming that if there are more than one real solution in any of the above intervals, then, by varying the parameter B , we can get a function that violates Theorem B.2.

Next, we will show that $F(y)$ must has only simple real roots under certain conditions. Again, we would want to be able to show this by looking at the solutions of the following equation instead

$$y^2 = \frac{-(A \sin 2y - D \sin y)y}{\cos 2y} - \frac{C \cos y}{\cos 2y} + \frac{E}{\cos 2y} + B. \quad (75)$$

Therefore, we need to be sure that y would not be a root of $F(y) = 0$ if $\cos 2y = 0$ in order to do this. In fact, one can easily show that if none of the solutions of the following equations is a non-negative integer (i.e. $k_i \notin \mathbb{Z}^+$, $i = 1, 2, 3, 4$),

$$0 = -(A - \frac{D}{\sqrt{2}})(2k_1\pi + \pi/4) - \left[\frac{C}{\sqrt{2}} - E \right]; \quad (76)$$

$$0 = (A + \frac{D}{\sqrt{2}})(2k_2\pi + 3\pi/4) + \left[\frac{C}{\sqrt{2}} + E \right]; \quad (77)$$

$$0 = -(A + \frac{D}{\sqrt{2}})(2k_3\pi + 5\pi/4) + \left[\frac{C}{\sqrt{2}} + E \right]; \quad (78)$$

$$0 = (A - \frac{D}{\sqrt{2}})(2k_4\pi + 7\pi/4) - \left[\frac{C}{\sqrt{2}} - E \right]. \quad (79)$$

then y would not be a root of $F(y) = 0$ if $\cos 2y = 0$. Note that The above equations come from substituting $F(y)$ by $\cos 2y = 0$.

Now, we can look at the solutions of (75). Let $f(y)$ be the right hand side of

(75). Then one would find

$$\begin{aligned}
\lim_{y \rightarrow 0} f(y) &= B - C + E, \\
\lim_{y \rightarrow 2k\pi + \pi/4^-} f(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + \pi/4^+} f(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + 3\pi/4^-} f(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + 3\pi/4^+} f(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + 5\pi/4^-} f(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + 5\pi/4^+} f(y) &= \infty, \\
\lim_{y \rightarrow 2k\pi + 7\pi/4^-} f(y) &= -\infty, \\
\lim_{y \rightarrow 2k\pi + 7\pi/4^+} f(y) &= \infty.
\end{aligned}$$

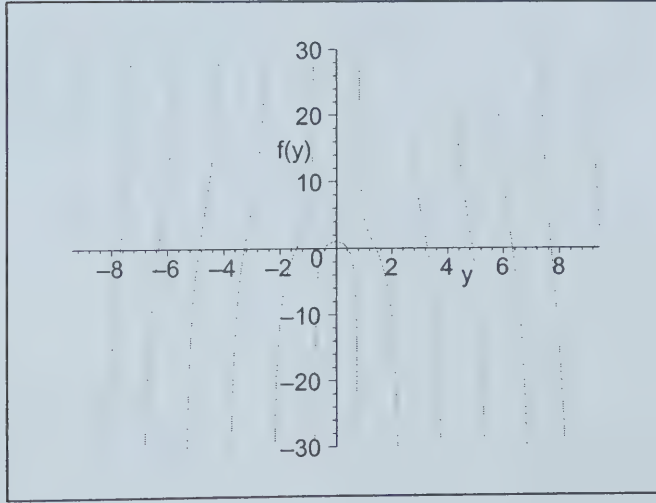


Figure 5: $A > C, D$: The graph of $f(y)$ with $A = 3$, $B = 1$, $C = 1$, $D = 1$, and $E = 1$.

Thus, if $(B - C + E) > 0$, (the function y^2 will intersect $f(y)$ at least 4 times in each of these intervals $[2k\pi, 2k\pi + 2\pi]$, where $k = 0, 1, 2, \dots$.

Since, the principle terms of $G(y)$ is $-y^2 \cos 2y$, we may choose ε to be 0. Then, similarly, one should be able to show that $F(y)$ has exactly $8k + 2$ real roots for k sufficiently large and this shows that all roots of $F(y)$ are real and simple when

$$(B - C + E) > 0.$$

At this point, it is clear that we are trying to use condition (a) in Theorem B.3 to get some result. Therefore, the easiest way to guarantee that the zeros of $F(y)$ and $G(y)$ are alternate is to have the following conditions satisfied:

$$g(y) > f(y) \quad \text{when} \quad y \in (2k\pi, 2k\pi + \pi/4), \quad (80)$$

$$g(y) < f(y) \quad \text{when} \quad y \in (2k\pi + \pi/4, 2k\pi + \pi/2), \quad (81)$$

$$g(y) > f(y) \quad \text{when} \quad y \in (2k\pi + \pi/2, 2k\pi + 3\pi/4), \quad (82)$$

$$g(y) < f(y) \quad \text{when} \quad y \in (2k\pi + 3\pi/4, 2k\pi + \pi), \quad (83)$$

$$g(y) > f(y) \quad \text{when} \quad y \in (2k\pi + \pi, 2k\pi + 5\pi/4), \quad (84)$$

$$g(y) < f(y) \quad \text{when} \quad y \in (2k\pi + 5\pi/4, 2k\pi + 3\pi/2), \quad (85)$$

$$g(y) > f(y) \quad \text{when} \quad y \in (2k\pi + 3\pi/2, 2k\pi + 7\pi/4), \quad (86)$$

$$g(y) < f(y) \quad \text{when} \quad y \in (2k\pi + 7\pi/4, 2k\pi + 2\pi). \quad (87)$$

But, we find that

$$g(y) - f(y) = \frac{1}{\cos 2y} \left[\frac{y(A - D \cos y)}{\sin 2y} + \frac{C}{2 \cos y} - E \right].$$

So, let us look at $g(y) - f(y)$ in $I = (2k\pi, 2k\pi + \pi/4)$. Since $\cos 2y > 0$, $\sin 2y > 0$ and $\cos y > 0$ in I , we have

$$\begin{aligned} & \frac{y(A - D \cos y)}{\sin 2y} + \frac{C}{2 \cos y} - E \\ & > \frac{2k\pi(A - D)}{1} + \frac{C}{2} - E \\ & > 2k\pi(A - D) + \frac{C}{2} - E. \end{aligned}$$

Thus, $g(y) > f(y)$ if $2k\pi(A - D) + \frac{C}{2} - E > 0$. However, it is easy to see that this condition must be satisfied when k is big enough, since $(A - D) > 0$ by assumption. Similarly, if we do the same analysis for $g(y) - f(y)$ in each of the intervals (80)-(87), we would see that in order to have all the inequalities (80)-(87) satisfied, the

following would be the sufficient conditions:

$$0 < 2k\pi(A - D) + \left[\frac{C}{2} - E \right], \quad (88)$$

$$0 < (2k\pi + \pi/4) \left(A - \frac{D}{\sqrt{2}} \right) + \left[\frac{C}{\sqrt{2}} - E \right], \quad (89)$$

$$0 > -(2k\pi + \pi/2)A - \left[\frac{C}{\sqrt{2}} + E \right], \quad (90)$$

$$0 > -(2k\pi + 3\pi/4) \left(A + \frac{D}{\sqrt{2}} \right) - \left[\frac{C}{2} + E \right], \quad (91)$$

$$0 < (2k\pi + \pi) \left(A + \frac{D}{\sqrt{2}} \right) - \left[\frac{C}{\sqrt{2}} + E \right], \quad (92)$$

$$0 < \frac{1}{\sqrt{2}}(2k\pi + 5\pi/4)A - \left[\frac{C}{\sqrt{2}} + E \right], \quad (93)$$

$$0 > -(2k\pi + 3\pi/2) \left(A - \frac{D}{\sqrt{2}} \right) + C, \quad (94)$$

$$0 > -(2k\pi + 7\pi/4)(A - D) + \left[\frac{C}{\sqrt{2}} - E \right]. \quad (95)$$

Obviously, they all can be satisfied when k is big enough. Therefore, the zeros of $F(y)$ and $G(y)$ must be alternate when k is big enough.

Finally, since $G'(0)F(0) = (A - D - C + 2B)(B - C + E)$ we have the following result.

Theorem 3.6 *Suppose the transcendental equation $T(z) = (z^2 + Az + B)e^{2z} + Ce^z + Dze^z + E$ satisfies the following:*

- (a) *all the parameters are positive;*
- (b) *$A > C$ and $A > D$; and*
- (c) *none of the solutions of any of the equations (76)-(79) is a non-negative integer.*

Then a necessary and sufficient condition that all the roots of $T(z)$ lie to the left of the imaginary axis is that

- (i) $A - D - C + 2B > 0$;
- (ii) $B - C + E > 0$; and
- (iii) *the finite numbers of roots of $G(y)$ and $F(y)$ contained in the finite interval $[0, m]$, the number $m > 0$ is determined in the proof, are alternate.*

3.4 Summary

In this section, we have studied two types of second-order elementary transcendental equations. Firstly, we looked at equations with $N_2(z) = 0$, which are the kind of transcendental equations that we will see in Section 4. We managed to obtain a necessary and sufficient conditions that with the help of available mathematical software, such as Maple and MATLAB, can easily be used to determine whether all zeros of the transcendental function lie in the left half of the complex plane. This then helps us solve the stability problem that links to this type of equations. Actually, we will illustrate the use of our results in Section 4 with an example. In the second part, we looked at equations with $N_2(z) \neq 0$, which are also the kind of transcendental equation that we will see in Section 5. Similarly, we have find a necessary and sufficient condition under which all zeros of the function lie in the left half of the complex plane. However, it is only a partial solution. Because of the complexity of the problem, we could only do the analysis for the function with some restrictions imposed on the parameters. The difficulty was due to the additional exponential function e^{-2rz} in the equation, as we have seen, which had highly complicated the functions that we needed to work with during our analysis. Again, we will look at an example in Section 5 to demonstrate the use of our results.

4 Zero Birth Patch

4.1 Model Equations

In this section, we look at a two patch model for which one of the patches has zero birth, namely, $b_2 \equiv 0$. For simplicity, we make the following assumptions:

$$d_{i,I} = d_I, \quad \text{for } i = 1, 2,$$

that is, the immature death rate is patch independent and

$$\sum_{i=1}^2 D_{ij,I} = 0, \quad \text{for } i = 1, 2,$$

that is, there is no loss of immature during migration. Thus,

$$M_I = \begin{bmatrix} -d_I - D_{21,I} & D_{12,I} \\ D_{21,I} & -d_I - D_{12,I} \end{bmatrix}$$

and

$$M_m = \begin{bmatrix} -D_{1m}^* & D_{12,m} \\ D_{21,m} & -D_{2m}^* \end{bmatrix}.$$

where $D_{1m}^* = d_{1,m} - D_{11,m}$, and $D_{2m}^* = d_{2,m} - D_{22,m}$.

Since we need to write the term $e^{M_I r}$ in model equation (8) explicitly, we should first diagonalize $M_I r$. We have

$$M_I r = \begin{bmatrix} -d_I r - D_{21,I} r & D_{12,I} r \\ D_{21,I} r & -d_I r - D_{12,I} r \end{bmatrix},$$

one can easily find that its eigenvalues are

$$\lambda_1 = -d_I r \quad \text{and} \quad \lambda_2 = -d_I r - \hat{D} r,$$

where $\hat{D} = D_{21,I} + D_{12,I}$, and the corresponding eigenvector is

$$v_1 = \begin{bmatrix} \frac{D_{12,I}}{D_{21,I}} \\ 1 \end{bmatrix} \quad \text{and} \quad v_2 = \begin{bmatrix} -1 \\ 1 \end{bmatrix},$$

respectively. Then, if we let

$$P = [v_1 \quad v_2] = \begin{bmatrix} \frac{D_{12,I}}{D_{21,I}} & -1 \\ 1 & 1 \end{bmatrix},$$

we get

$$P^{-1} = \hat{D}^{-1} \begin{bmatrix} D_{21,I} & D_{21,I} \\ -D_{21,I} & D_{12,I} \end{bmatrix}.$$

Also, we let

$$D = P^{-1}M_{Ir}P = \begin{bmatrix} -d_{Ir} & 0 \\ 0 & -(d_I + \hat{D})r \end{bmatrix}.$$

Then, we have

$$e^{M_{Ir}} = Pe^DP^{-1} = \hat{D}^{-1} \begin{bmatrix} D_{12,I}e^{-d_{Ir}} + D_{21,I}e^{-(d_I+\hat{D})r} & D_{12,I}(e^{-d_{Ir}} - e^{-(d_I+\hat{D})r}) \\ D_{21,I}(e^{-d_{Ir}} - e^{-(d_I+\hat{D})r}) & D_{21,I}e^{-d_{Ir}} + D_{12,I}e^{-(d_I+\hat{D})r} \end{bmatrix}.$$

Therefore, our model equation (8) would be

$$\begin{aligned} w'(t) &= \begin{bmatrix} -D_{1m}^* & D_{12,m} \\ D_{21,m} & -D_{2m}^* \end{bmatrix} w(t) \\ &+ \hat{D}^{-1} \begin{bmatrix} D_{12,I}e^{-d_{Ir}} + D_{21,I}e^{-(d_I+\hat{D})r} & D_{12,I}(e^{-d_{Ir}} - e^{-(d_I+\hat{D})r}) \\ D_{21,I}(e^{-d_{Ir}} - e^{-(d_I+\hat{D})r}) & D_{21,I}e^{-d_{Ir}} + D_{12,I}e^{-(d_I+\hat{D})r} \end{bmatrix} \\ &*b(w(t-r)), \end{aligned}$$

or equivalently,

$$w_1'(t) = -(d_{1,m} - D_{11,m})w_1(t) + D_{12,m}w_2(t) + e^*(1-r^*)b_1(w_1(t-r)), \quad (96)$$

$$w_2'(t) = -(d_{2,m} - D_{22,m})w_2(t) + D_{21,m}w_1(t) + e^*r^*b_1(w_1(t-r)), \quad (97)$$

where $e^* = e^{-d_{Ir}}$ and $r^* = \frac{D_{21,I}}{\hat{D}}[1 - e^{-r\hat{D}}]$. Note that $0 < e^*, r^* < 1$.

4.2 Equilibria

The equilibrium equations are:

$$0 = -D_{1m}^*w_1 + D_{12,m}w_2 + e^*(1-r^*)b_1(w_1), \quad (98)$$

$$0 = -D_{2m}^*w_2 + D_{21,m}w_1 + e^*r^*b_1(w_1), \quad (99)$$

where $D_{1m}^* = d_{1,m} - D_{11,m}$ and $D_{2m}^* = d_{2,m} - D_{22,m}$.

Clearly, (0,0) is a solution. Solving (98) and (99) for positive equilibrium, we get

$$\begin{aligned} \frac{D_{21,m}w_1 + e^*r^*b_1(w_1)}{D_{2m}^*} &= \frac{D_{1m}^*w_1 - e^*(1-r^*)b_1(w_1)}{D_{12,m}} \\ (D_{1m}^*D_{2m}^* - D_{21,m}D_{12,m})w_1 &= [d_{2,m}e^*(1-r^*) + D_{12,m}e^*]b_1(w_1) \\ w_1 &= \frac{1}{\beta_1} \ln \left[\frac{(d_{2,m}e^*(1-r^*) + D_{12,m}e^*)p_1}{D_{1m}^*D_{2m}^* - D_{21,m}D_{12,m}} \right] \\ &= \frac{1}{\beta_1} \ln(Mp_1), \end{aligned} \quad (100)$$

where $M = \frac{d_{2,m}e^*(1-r^*) + D_{12,m}e^*}{D_{1m}^*D_{2m}^* - D_{21,m}D_{12,m}}$. Substituting (100) into (99), we get

$$w_2 = \frac{1}{\beta_1} \ln(Mp_1) \frac{(D_{21,m} + e^*r^*M^{-1})}{D_{2m}^*}.$$

Thus, we have

Theorem 4.1 *The system of the two patch model for which one of the patches has zero birth has two equilibria when $Mp_1 > 1$:*

$$E_0 = (0, 0) \quad \text{and} \quad E_1 = (\bar{w}_1, \bar{w}_2),$$

$$\text{where } \bar{w}_1 = \frac{1}{\beta_1} \ln(Mp_1) \quad \text{and} \quad \bar{w}_2 = \frac{(D_{21,m} + e^*r^*M^{-1})}{D_{2m}^*} \bar{w}_1.$$

4.3 Stability

Linearizing (96) and (97) at an equilibrium (w_1^*, w_2^*) , we get

$$\begin{aligned} w_1'(t) &= -D_{1m}^*w_1(t) + D_{12,m}w_2(t) + e^*(1-r^*)b_1'(w_1^*)w_1(t-r), \\ w_2'(t) &= D_{21,m}w_1(t) - D_{2m}^*w_2(t) + e^*r^*b_1'(w_1^*)w_1(t-r). \end{aligned}$$

The stability of an equilibrium (w_1^*, w_2^*) is determined by the roots of the characteristic equation

$$\begin{aligned} 0 &= \begin{vmatrix} \lambda + D_{1m}^* - e^*(1-r^*)b_1'(w_1^*)e^{-\lambda r} & -D_{12,m} \\ -D_{21,m} - e^*r^*b_1'(w_1^*)e^{-\lambda r} & \lambda + D_{2m}^* \end{vmatrix} \\ &= [\lambda + D_{1m}^* - e^*(1-r^*)b_1'(w_1^*)e^{-\lambda r}][\lambda + D_{2m}^*] - D_{12,m}[D_{21,m} + e^*r^*b_1'(w_1^*)e^{-\lambda r}]. \end{aligned} \quad (101)$$

From this we get

$$\begin{aligned} 0 &= \lambda^2 + (D_{1m}^* + D_{2m}^*)\lambda + (D_{1m}^*D_{2m}^* - D_{12,m}D_{21,m}) \\ &\quad - (1-r^*)e^*b_1'(w_1^*)\lambda e^{-\lambda r} \\ &\quad - [D_{12,m} + d_{2,m}(1-r^*)]e^*b_1'(w_1^*)e^{-\lambda r}. \end{aligned} \quad (102)$$

Note that the characteristic equation (102) is of the form:

$$\lambda^2 + A\lambda + B + (C\lambda + D)e^{-r\lambda} = 0,$$

where A, B, C , and D are real and $A, B > 0$.

This is the type of transcendental equations that we have studied in Section 3.2. We now illustrate the use of the Theorems in Section 3.2 with an example.

EXAMPLE 4.1

We pick our model parameters as follows:

Immature parameters:

$$\begin{cases} d_{1,I} = d_{2,I} = d_I = 0.03, \\ D_{21,I} = -D_{11,I} = 0.009, \\ D_{12,I} = -D_{22,I} = 0.015. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.08, \\ d_{2,m} = 0.06, \\ D_{21,m} = -D_{11,m} = 0.012, \\ D_{12,m} = -D_{22,m} = 0.008. \end{cases}$$

Birth functions:

$$\begin{cases} b_1(w) = 2we^{-w}, \\ b_2(w) \equiv 0. \end{cases}$$

Let us choose the maturation time to be $r = 10$. Then, using Maple, we have

$$\begin{aligned} e^* &\cong 0.74082, \\ r^* &\cong 0.08001, \\ M &\cong 7.60050. \end{aligned}$$

Also, the equilibria would be

$$E_0 = (0, 0) \quad \text{and} \quad E_1 \cong (2.72136, 0.79236).$$

Therefore, at $E_0 = (0, 0)$, the characteristic equation (102) is

$$\lambda^2 + \tilde{A}\lambda + \tilde{B} + (\tilde{C}\lambda + \tilde{D})e^{-r\lambda} = 0,$$

where $\tilde{A} = 0.16$, $\tilde{B} = 0.00616$, $\tilde{C} \cong -1.36308$, and $\tilde{D} \cong -0.93638$. In order to use the Theorems in section (3.2), we need to do this translations:

$$\begin{aligned} A &:= \tilde{A}r = 1.6, \\ B &:= \tilde{B}r^2 = 0.616, \\ C &:= \tilde{C}r \cong -13.63084, \\ D &:= \tilde{D}r^2 \cong -9.36381. \end{aligned}$$

Then, we can tell immediately by Theorem 3.3 that E_0 is **unstable** since $A + B + C$ is obviously less than 0.

Similarly, at $E_1 \cong (2.72136, 0.79236)$, the characteristic equation (102) is

$$\lambda^2 + \tilde{A}\lambda + \tilde{B} + (\tilde{C}\lambda + \tilde{D})e^{-r\lambda} = 0,$$

where $\tilde{A} = 0.16$, $\tilde{B} = 0.00616$, $\tilde{C} \cong 0.15436$, and $\tilde{D} \cong 0.01060$. Again, we do the translations:

$$\begin{aligned} A &:= \tilde{A}r &= 1.6, \\ B &:= \tilde{B}r^2 &= 0.616, \\ C &:= \tilde{C}r &\cong 1.54356, \\ D &:= \tilde{D}r^2 &\cong 1.06036. \end{aligned}$$

Apparently, we can apply Theorem 3.1 to our characteristic equation. Therefore, we should use the procedure associated with Theorem 3.1, which is given at page 25, to get a conclusion. Note that we use Maple for all the numerical computations below.

Step 1: $B + D$ is obviously positive.

Step 2: We may pick $k' = 1$, then we get $a_{odd} \cong 6.74658 \in (2\pi, 3\pi)$ and $a_{even} \cong 9.43080 \in (3\pi, 4\pi)$.

Step 3: We have $\alpha = \cos(a_{odd}) \cong 0.89454$. Since $(A + 1)C > 0$, so we may pick $m_1 = 0$. Also, since $AC - D > 0$, we have to choose m_2 such that $m_2^2 > -0.46347$, thus we may pick $m_2 = 0$. Therefore, we would have $\bar{k} = 1$ and we need to check the condition $G'(y)F(y)$ for the sole root $y \in (0, \pi)$ only. We can find that the root is $y \cong 1.70417$ and $G'(y)F(y) \cong 5.94718 > 0$.

Step 4: We have $\beta = \cos(a_{even}) \cong -0.99998$. Following a few simple calculations and selections, we would have $m_1 = 1$ and $m_2 = 0$. Therefore, we have $\bar{k} = 1$ and we need to check the condition $G'(y)F(y)$ for the sole root $y \in (\pi, 2\pi)$ only. We can find that the root is $y \cong 3.16053$ and $G'(y)F(y) \cong 100.33184 > 0$.

Thus, according to Theorem 3.1, we can conclude that E_1 is **stable**.

4.4 Summary

In this section, we have looked at a two patch model for which one of the patches has zero birth. We have shown that this model can have an unique non-trivial equilibrium. For the stability analysis, we realized that the associated characteristic

equation is a second degree transcendental equation that has been discussed in Section 3.2. At last, we have looked at an example and used the Theorems in Section 3.2 to solve our stability problem.

5 Immobile Immature

5.1 Model Equations

In this section, we consider a two-patch model such that the immature are immobile. Consequently, $D_{ij,I} = 0$, for $i, j = 1, 2$. Then, our model equation (8) becomes

$$w'(t) = \begin{bmatrix} -d_{1,m} + D_{11,m} & D_{12,m} \\ D_{21,m} & -d_{2,m} + D_{22,m} \end{bmatrix} w(t) + \begin{bmatrix} e^{-d_{1,I}r} & 0 \\ 0 & e^{-d_{2,I}r} \end{bmatrix} b(w(t-r)),$$

or equivalently,

$$w'_1(t) = -D_{1m}^* w_1(t) + D_{12,m} w_2(t) + e^{-d_{1,I}r} b_1(w_1(t-r)), \quad (103)$$

$$w'_2(t) = D_{21,m} w_1(t) - D_{2m}^* w_2(t) + e^{-d_{2,I}r} b_2(w_2(t-r)), \quad (104)$$

where $D_{1m}^* = d_{1,m} - D_{11,m}$ and $D_{2m}^* = d_{2,m} - D_{22,m}$. We shall assume that $D_{12,m} > 0$ and $D_{21,m} > 0$.

5.2 Equilibria

The equilibrium equations are:

$$0 = -D_{1m}^* w_1 + D_{12,m} w_2 + e^{-d_{1,I}r} b_1(w_1), \quad (105)$$

$$0 = D_{21,m} w_1 - D_{2m}^* w_2 + e^{-d_{2,I}r} b_2(w_2). \quad (106)$$

Clearly, this system of equations is of the form

$$a_1 w_1 = a_2 w_2 + a_3 b_1(w_1), \quad (107)$$

$$c_2 w_2 = c_1 w_1 + c_3 b_2(w_2), \quad (108)$$

where a_i and $c_i > 0$.

We are going to study the system (107)-(108) and show that which cannot have more than one positive solution (i.e. (w_1, w_2) with $w_1 > 0$ and $w_2 > 0$). Recall that $b_i(w) = p_i w e^{-\beta_i w}$ and $b'_i(w) = p_i e^{-\beta_i w} (1 - \beta_i w)$. Most of the arguments of the analysis below depend mainly on the properties of the function $b_i(w) = p_i w e^{-\beta_i w}$, one should refer to the appendix for details.

let us consider equation (107), our idea is to construct a function $h_1(w_2) = w_1$ for $w_2 \geq 0$ such that every point on this curve satisfies equation (107) and vice versa for $w_2 > 0$. But this is easy, since we only need to think of w_2 in (107) as a non-negative parameter and $h_1(w_2)$ to be the unique positive solution of the equation $a_1 w_1 = a_3 b_1(w_1) + a_2 w_2$ (in the case of $w_2 = 0$, we choose $h_1(w_2) = 0$ if there is no positive solution (i.e. when $a_1 \geq a_3 p_1$)). Therefore, by defining $h_1(w_2)$ for $w_2 \geq 0$ this way, we have

Case 1) $a_1 \geq a_3 p_1$

$$h_1(w_2) = w_1 \text{ satisfies (107) and } h_1(0) = 0.$$

Case 2) $a_1 < a_3 p_1$

$$h_1(w_2) = w_1 \text{ satisfies (107) and } h_1(0) > 0.$$

Properties of $h_1(w_2)$:

First, one should see that $h(w_2)$ is an increasing function and $\lim_{w_2 \rightarrow \infty} h_1(w_2) = \infty$. Also, $h'_1(w_2)$ can be obtained by differentiate (107) implicitly respect to w_2 :

$$\begin{aligned} a_1 \frac{dw_1}{dw_2} &= a_2 + a_3 b'_1(w_1) \frac{dw_1}{dw_2} \\ \frac{dw_1}{dw_2} &= \frac{a_2}{a_1 - a_3 b'_1(w_1)} \\ h'_1(w_2) &= \frac{a_2}{a_1 - a_3 b'_1(h_1(w_2))} > 0. \end{aligned}$$

Note that $a_1 - a_3 b'_1(h_1(w_2)) > 0$ since $h_1(w_2) = w_1$ satisfies (107), so $h'_1(w_2) > 0$, which is consistent with the comment above.

We can see that

$$\lim_{w_2 \rightarrow \infty} h'_1(w_2) = \frac{a_2}{a_1}. \quad (109)$$

Also, one can find that

$$h''_1(w_2) = \frac{a_2 a_3 h'_1(w_2)}{(a_1 - a_3 b'_1(h_1(w_2)))^2} b''_1(h_1(w_2)),$$

where

$$b''_1(h_1(w_2)) = p_1 \beta_1 e^{-\beta_1 h_1(w_2)} [\beta_1 h_1(w_2) - 2].$$

Thus,

$$h''_1(w_2) = M [\beta_1 h_1(w_2) - 2], \quad (110)$$

where M is a positive number.

Comment: since $h_1(w_2)$ is an increasing function, therefore, either $h_1''(w_2)$ is positive the whole time or it is negative at first and eventually positive for the rest.

Next, we consider equation (108). Similarly, we want to solve w_1 in terms of w_2 . We would get

$$w_1 = \frac{1}{c_1}(c_2w_2 - c_3b_2(w_2)).$$

Therefore, we define

$$h_2(w_2) = \frac{1}{c_1}(c_2w_2 - c_3b_2(w_2)).$$

However, one should see that $h(w_2)$ may not be ≥ 0 for all $w_2 \geq 0$, thus, the domain should be chosen as follow:

Case 1) $c_2 \geq c_3p_2$

$$h_2(w_2) = w_1 \text{ is defined on } [0, \infty) \text{ and } h_2(0) = 0.$$

Case 2) $c_2 < c_3p_2$

Let w_2^* to be the unique positive solution of the equation $c_2w_2 = c_3b_2(w_2)$.

Then, $h_2(w_2) = w_1$ is defined on $[w_2^*, \infty)$ and $h_2(w_2^*) = 0$.

Clearly, for $w_1, w_2 > 0$, (w_1, w_2) is a point on (108) if and only if it is a point on $(h_2(w_2), w_2)$ as well.

Properties of $h_2(w_2)$:

Same as $h_1(w_2)$, $h_2(w_2)$ is an increasing function and $\lim_{w_2 \rightarrow \infty} h_2(w_2) = \infty$.

$$h_2'(w_2) = \frac{1}{c_1}(c_2 - c_3b_2'(w_2)) > 0$$

and

$$\lim_{w_2 \rightarrow \infty} h_2'(w_2) = \frac{c_2}{c_1}. \quad (111)$$

Also,

$$\begin{aligned} h_2''(w_2) &= -\frac{c_3}{c_1}b_2''(w_2) \\ &= -\frac{c_3}{c_1}p_2\beta_2e^{-\beta_2w_2}[\beta_2w_2 - 2] \\ &= N(2 - \beta_2w_2), \end{aligned} \quad (112)$$

where N is a positive number.

Comment: It is easy to see that either $h_2''(w_2)$ is positive at first and eventually negative for the rest or it is always negative in its domain.

With everything in place, we can prove the following:

Claim: The system of equations (107)-(108) has an unique positive solution iff $\frac{c_2}{c_1} > \frac{a_2}{a_1}$ and one of the following conditions is satisfied:

1. $a_1 \geq a_3p_1$, $c_2 \geq c_3p_2$, and $\frac{c_2 - c_3p_2}{c_1} < \frac{a_2}{a_1 - a_3p_1}$.
2. $a_1 < a_3p_1$ or $c_2 < c_3p_2$.

Note that $\frac{a_2}{a_1 - a_3p_1}$ can be infinity.

Proof: The idea is to show that the functions $h_1(w_2)$ and $h_2(w_2)$ can or cannot have a positive intersection in various cases.

Case 1) $\frac{c_2}{c_1} \leq \frac{a_2}{a_1}$

By (107) and (108), we have

$$a_1h_1(w_2) = a_2w_2 + a_3b_1(h_1(w_2))$$

and

$$c_2w_2 = c_1h_2(w_2) + c_3b_2(w_2).$$

Thus,

$$h_1(w_2) = \frac{a_2w_2 + a_3b_1(h_1(w_2))}{a_1}$$

and

$$-h_2(w_2) = \frac{-c_2w_2 + c_3b_2(w_2)}{c_1}.$$

So,

$$h_1(w_2) - h_2(w_2) = \frac{(a_2c_1 - a_1c_2)w_2 + a_3c_1b_1(h_1(w_2)) + a_1c_3b_2(w_2)}{a_1c_1} > 0, \text{ for } w_2 > 0.$$

This is because $(a_2c_1 - a_1c_2) \geq 0$, $b_1(h_1(w_2)) > 0$, and $b_2(w_2) > 0$ for $w_2 > 0$.

For the following cases we shall assume $\frac{c_2}{c_1} > \frac{a_2}{a_1}$.

Case 2) $a_1 \geq a_3p_1$ and $c_2 \geq c_3p_2$

Suppose $\frac{c_2 - c_3p_2}{c_1} < \frac{a_2}{a_1 - a_3p_1}$, with the assumptions $a_1 \geq a_3p_1$ and $c_2 \geq c_3p_2$, we have $h_1(0) = h_2(0) = 0$, but since

$$h_1'(0) = \frac{a_2}{a_1 - a_3p_1} > \frac{c_2 - c_3p_2}{c_1} = h_2'(0),$$

there must exist an interval $I = (0, k)$, $k > 0$ such that $h_1 > h_2$ in I . However, since $\frac{c_2}{c_1} > \frac{a_2}{a_1}$, by (109) and (111), $h_1(w_2)$ and $h_2(w_2)$ must intersect at least once for $w_2 > 0$. This shows existence.

For the uniqueness, one should consider the derivatives of h_1 and h_2 at the first intersection. Assume $w_2^* > 0$ be the first intersection, then by (107) and (108), we must have

$$\begin{aligned} a_1 h_1(w_2^*) &= a_2 w_2^* + a_3 p_1 h_1(w_2^*) e^{-\beta_1 h_1(w_2^*)}, \\ c_2 w_2^* &= c_1 h_2(w_2^*) + c_3 p_2 w_2^* e^{-\beta_2 w_2^*}, \end{aligned}$$

or equivalently,

$$\begin{aligned} a_1 &= a_2 \frac{w_2^*}{h_1(w_2^*)} + a_3 p_1 e^{-\beta_1 h_1(w_2^*)}, \\ c_2 &= c_1 \frac{h_2(w_2^*)}{w_2^*} + c_3 p_2 e^{-\beta_2 w_2^*}. \end{aligned}$$

Therefore,

$$\frac{c_2 - c_3 p_2 e^{-\beta_1 w_2^*}}{c_1} = \frac{a_2}{a_1 - a_3 p_1 e^{-\beta_1 h_1(w_2^*)}}. \quad (113)$$

From (113), we can see that

$$\begin{aligned} h_2'(w_2^*) &= \frac{c_2 - c_3 p_2 e^{-\beta_1 w_2^*} (1 - \beta_2 w_2^*)}{c_1} \\ &> \frac{c_2 - c_3 p_2 e^{-\beta_1 w_2^*}}{c_1} \\ &> \frac{a_2}{a_1}, \end{aligned} \quad (114)$$

since $(1 - \beta_2 w_2^*) < 1$ and $a_1 - a_3 p_1 e^{-\beta_1 h_1(w_2^*)} > 0$.

Similarly,

$$\begin{aligned}
h'_1(w_2^*) &= \frac{a_2}{a_1 - a_3 p_1 e^{-\beta_1 h_1(w_2^*)} (1 - \beta_1 h_1(w_2^*))} \\
&< \frac{a_2}{a_1 - a_3 p_1 e^{-\beta_1 h_1(w_2^*)}} \\
&< \frac{c_2}{c_1}.
\end{aligned} \tag{115}$$

Finally, knowing (114) and (115), it is easy to use (110) and (112) to argue that no intersection is possible after the first one.

On the other hand, suppose $\frac{c_2 - c_3 p_2}{c_1} \geq \frac{a_2}{a_1 - a_3 p_1}$, clearly, we will have $h'_2(0) > h'_1(0)$. Therefore, by (110) and (112), $h_2 > h_1$ for $w_2 > 0$. No positive intersection is possible.

Case 3) $a_1 < a_3 p_1$ or $c_2 < c_3 p_2$,

Because the domain of $h_2(w_2)$ is $[w^*, \infty)$, where $w^* \geq 0$, then, by how we defined h_1 and h_2 , we must have $h_1(w^*) > h_2(w^*)$. Therefore, h_1 and h_2 must have a unique positive intersection for the same argument as in **Case 2**. $\square$

Therefore, for our equilibrium equations (105) and (106), we get the following conclusion. Note that $\frac{D_{2m}^*}{D_{21,m}} > \frac{D_{12,m}}{D_{1m}^*}$ is always true, so that the condition $\frac{c_2}{c_1} > \frac{a_2}{a_1}$ is guaranteed.

Theorem 5.1 *The two-patch immobile immature model has a unique positive equilibrium as well as the trivial equilibrium $(0, 0)$ if and only if one of the following conditions is satisfied:*

- (i) $D_{1m}^* \geq p_1 e^{-d_{1,1}r}$, $D_{2m}^* \geq p_2 e^{-d_{2,1}r}$, and $\frac{D_{2m}^* - p_2 e^{-d_{2,1}r}}{D_{21,m}} < \frac{D_{12,m}}{D_{1m}^* - p_1 e^{-d_{1,1}r}}$.
- (ii) $D_{1m}^* < p_1 e^{-d_{1,1}r}$ or $D_{2m}^* < p_2 e^{-d_{2,1}r}$.

5.3 Stability

Linearizing (103) and (104) at an equilibrium (w_1^*, w_2^*) , we get

$$\begin{aligned} w_1'(t) &= -D_{1m}^* w_1(t) + D_{12,m} w_2(t) + e^{-d_{1,1r}} b_1'(w_1^*) w_1(t-r), \\ w_2'(t) &= D_{21,m} w_1(t) - D_{2m}^* w_2(t) + e^{-d_{2,1r}} b_2'(w_2^*) w_2(t-r). \end{aligned}$$

Thus, the stability of an equilibrium (w_1^*, w_2^*) is determined by the roots of the characteristic equation

$$\begin{aligned} 0 &= \begin{vmatrix} \lambda + D_{1m}^* - e^{-d_{1,1r}} b_1'(w_1^*) e^{-\lambda r} & -D_{12,m} \\ -D_{21,m} & \lambda + D_{2m}^* - e^{-d_{2,1r}} b_2'(w_2^*) e^{-\lambda r} \end{vmatrix} \\ &= [\lambda + D_{1m}^* - e^{-d_{1,1r}} b_1'(w_1^*) e^{-\lambda r}][\lambda + D_{2m}^* - e^{-d_{2,1r}} b_2'(w_2^*) e^{-\lambda r}] - D_{21,m} D_{12,m} \\ &= [\lambda + D_{1m}^* - K_1 e^{-\lambda r}][\lambda + D_{2m}^* - K_2 e^{-\lambda r}] - D_{21,m} D_{12,m}. \end{aligned}$$

Or equivalently,

$$\begin{aligned} 0 &= \lambda^2 + (D_{1m}^* + D_{2m}^*)\lambda + (D_{1m}^* D_{2m}^* - D_{12,m} D_{21,m}) \\ &\quad - (D_{1m}^* K_2 + D_{2m}^* K_1) e^{-\lambda r} - (K_1 + K_2) \lambda e^{-\lambda r} + K_1 K_2 e^{-\lambda 2r}, \end{aligned} \quad (116)$$

where $K_1 = e^{-d_{1,1r}} b_1'(w_1^*)$ and $K_2 = e^{-d_{2,1r}} b_2'(w_2^*)$.

The is the type of characteristic equation we have discussed in Section 3.3, however, we could only have found a partial solution to the problem. Therefore, before we illustrate the use of the Theorem 3.6 with an example, we will look at a completely different approach from the one in Section 3.2 and see if we can obtain more information about the stability of the equilibria.

The characteristic equation (116) can be written in the following form:

$$0 = [\lambda + D_{1m}^* - K_1 e^{-\lambda r}][\lambda + D_{2m}^* - K_2 e^{-\lambda r}] - D_{21,m} D_{12,m}. \quad (117)$$

Instead of analyzing (117) with r as the delay, we consider the following equation:

$$0 = [\lambda + D_{1m}^* - K_1 e^{-\lambda T}][\lambda + D_{2m}^* - K_2 e^{-\lambda T}] - D_{21,m} D_{12,m}. \quad (118)$$

One should realize that K_1 and K_2 still depend on r and the idea is to obtain sufficient conditions to not allow (118) to have any stability switching (any root crossing the imaginary axis) by increasing T from 0 to r with r fixed. This can give us sufficient conditions for the equilibria to be stable.

First, we should look at the roots of (118) when $T = 0$. When $T = 0$, we have

$$\begin{aligned}
0 &= [\lambda + D_{1m}^* - K_1][\lambda + D_{2m}^* - K_2] - D_{21,m}D_{12,m} \\
0 &= \lambda^2 + [D_{1m}^* + D_{2m}^* - (K_1 + K_2)]\lambda + [(D_{1m}^* - K_1)(D_{2m}^* - K_2) - D_{12,m}D_{21,m}] \\
\lambda &= \frac{-[D_{1m}^* + D_{2m}^* - (K_1 + K_2)]}{2} \\
&\quad \pm \frac{\sqrt{[D_{1m}^* + D_{2m}^* - (K_1 + K_2)]^2 - 4[(D_{1m}^* - K_1)(D_{2m}^* - K_2) - D_{12,m}D_{21,m}]}}{2}.
\end{aligned} \tag{119}$$

Clearly, from (119), we see that $\text{Re}(\lambda) < 0$ if and only if

$$(D_{1m}^* - K_1)(D_{2m}^* - K_2) > D_{12,m}D_{21,m}. \tag{120}$$

Now, we find a sufficient conditions to make stability switching impossible. Let $\lambda = iy$, $y \neq 0$ to be a root of (118), then

$$\begin{aligned}
|D_{21,m}D_{12,m}|^2 &= |[iy + D_{1m}^* - K_1e^{-iT y}][iy + D_{2m}^* - K_2e^{-iT y}]|^2 \\
D_{12,m}^2 D_{21,m}^2 &= [(D_{1m}^* - K_1 \cos Ty)^2 + (y + K_1 \sin Ty)^2] \\
&\quad * [(D_{2m}^* - K_2 \cos Ty)^2 + (y + K_2 \sin Ty)^2].
\end{aligned} \tag{121}$$

But, since the right hand side of (121) is greater than

$$\begin{aligned}
&(D_{1m}^* - K_1 \cos Ty)^2 (D_{2m}^* - K_2 \cos Ty)^2 \\
&> (D_{1m}^* - |K_1|)^2 (D_{2m}^* - |K_2|)^2.
\end{aligned}$$

Thus, if

$$(D_{1m}^* - |K_1|)^2 (D_{2m}^* - |K_2|)^2 \geq D_{12,m}^2 D_{21,m}^2, \tag{122}$$

then equation (118) cannot have any pure imaginary root for $T \in [0, r]$.

By combining the results above and applying lemma B.1 in appendix B. We can conclude that if conditions (120) and (122) are satisfied, then equation (117) has all zeros lie in the left half of the complex plane. Or equivalently, for an equilibrium (w_1^*, w_2^*) , if conditions (120) and (122) are satisfied, then it must be stable.

Applying this result to our stability problem, we have the following conclusion:

Theorem 5.2 *The trivial equilibrium $(0, 0)$ must be stable if one of the following conditions is satisfied*

- (i) $D_{1m}^* \geq e^{-d_{1,I}r} p_1$, $D_{2m}^* \geq e^{-d_{2,I}r} p_2$ and there is no positive equilibrium, or
- (ii) $D_{1m}^* < e^{-d_{1,I}r} p_1$ and $(D_{1m}^* - e^{-d_{1,I}r} p_1)(D_{2m}^* - e^{-d_{2,I}r} p_2) > D_{12,m} D_{21,m}$, or
- (iii) $D_{2m}^* < e^{-d_{2,I}r} p_2$ and $(D_{1m}^* - e^{-d_{1,I}r} p_1)(D_{2m}^* - e^{-d_{2,I}r} p_2) > D_{12,m} D_{21,m}$.

Theorem 5.3 *The positive equilibrium (w_1^*, w_2^*) is stable if the following conditions are satisfied*

- (i) $[D_{1m}^* - e^{-d_{1,I}r} b_1'(w_1^*)][D_{2m}^* - e^{-d_{2,I}r} b_2'(w_2^*)] \geq D_{12,m} D_{21,m}$, and
- (ii) $[D_{1m}^* - e^{-d_{1,I}r} |b_1'(w_1^*)|]^2 [D_{2m}^* - e^{-d_{2,I}r} |b_2'(w_2^*)|]^2 \geq D_{12,m}^2 D_{21,m}^2$.

As we can see, the informations we have obtained above is limited and sometimes it may not be useful. This is all deal to the complexity which has been introduced by the additional exponential function $e^{-\lambda_2 r}$ in the characteristic equation (116). Now, we should turn to our result in section 3.3 and look at an example.

EXAMPLE 5.1

We pick our model parameters as follows:

Immature parameters:

$$\begin{cases} d_{1,I} = 0.03, \\ d_{2,I} = 0.04, \\ D_{ij,I} = 0, \quad 1 \leq i, j \leq 2. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.08, \\ d_{2,m} = 0.06, \\ D_{21,m} = -D_{11,m} = 0.012, \\ D_{12,m} = -D_{22,m} = 0.008. \end{cases}$$

Birth functions:

$$\begin{cases} b_1(w) = 0.8we^{-w}, \\ b_2(w) = 0.2we^{-1.3w}. \end{cases}$$

Let us choose the maturation time to be $r = 10$. Then, using Maple, we could find that the positive equilibria is

$$E_1 \cong (1.90422, 0.88795).$$

Therefore, at E_1 , the characteristic equation (116) is

$$0 = \lambda^2 + \tilde{A}\lambda + \tilde{B} + \tilde{C}e^{-\lambda r} + \tilde{D}\lambda e^{-\lambda r} + \tilde{E}e^{-\lambda 2r},$$

where $\tilde{A} = 0.16$, $\tilde{B} = 0.00616$, $\tilde{C} \cong 0.00603$, $\tilde{D} \cong -0.08634$, and $\tilde{E} = 0.00052$. In order to use Theorem 3.6, we need to do this translations:

$$\begin{aligned} A &:= \tilde{A}r = 1.6, \\ B &:= \tilde{B}r^2 = 0.616, \\ C &:= \tilde{C}r \cong 0.60275, \\ D &:= \tilde{D}r^2 \cong 0.86338, \\ E &:= \tilde{E}r^2 \cong 0.05206. \end{aligned}$$

First, we need to check the conditions (a)-(c) in Theorem 3.6. Conditions (a) and (b) are obviously satisfied. About condition (c), we can easily check that the solutions of (76)-(79) of this system are all negative, thus, it is satisfied as well.

Now we can look at conditions (1)-(3) and get a conclusion. We have $A - D - C + 2B \cong 1.36587 > 0$ and $B - C + E \cong 0.065311 > 0$, so conditions (1) and (2) are satisfied. Then, according to condition (3), we should find the finite interval $(0, m)$ on which we need to inspect every roots of $G(y)$ and $F(y)$. Therefore, if we trace back to the analysis, we see that all we need to find is a non-negative number k' such that $\forall k \geq k'$ the inequalities (88)-(95) are satisfied and this will give us the finite interval we want, which will be $(0, 2k'\pi)$. For this example, after some simple calculations, we can see that k' can be chosen to be 0 and therefore the finite interval we need will be $(0, 0)$, which means no inspection is necessary (i.e. the roots of $G(y)$ and $F(y)$ are guaranteed to be alternating). Figure 6 is the graph of $g(y)$ and $f(y)$ which were defined in the analysis of Theorem 3.6, which also gives evidence that the roots of $G(y)$ and $F(y)$ are alternating. Thus, by Theorem 3.6, we can conclude that E_1 is stable.

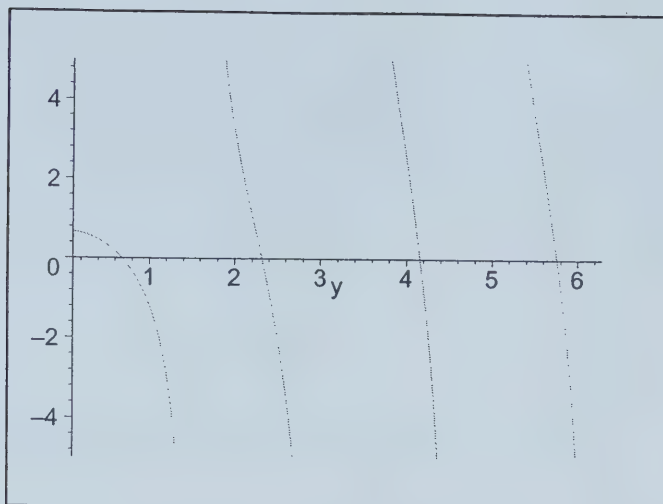


Figure 6: *EXAMPLE 5.1*: The graph of $g(y)$ and $f(y)$: $g(y)$ —solid line; $f(y)$ —dashline

5.4 Summary

In this section, we have looked at a two patch model for which the immature are immobile. We were managed to show that this system can have a unique non-trivial equilibrium. Also, by studying the stabilities of the equilibria, we realized that the associated characteristic equation is highly complicated, even when there are only two different exponential functions in the equation. Therefore, in addition to the partial solution to the equation found in Section 3.3, we tried with a different approach to obtain some more useful informations about stabilities of the equilibria. Then, we finished the section with an example to illustrate the use of Theorem 3.6 in Section 3.3.

6 Numerical Results

We will look at some numerical simulations of the models we have discussed before. For the one-way migration model, we will emphasis on showing the existence of periodic solutions. For the other two models, we will first do the simulations for the examples which we have discussed in the end of Section 4 and Section 5, then we try on some different parameters and make some observations. All the numerical simulations in this section is obtained by using DDE23(MATLAB base)[16].

6.1 One-Way Migration Model

Simulation 1.1

In this simulation, we will look at the stability of the equilibria. We consider a model with the following parameters:

Immature parameters:

$$\left\{ \begin{array}{l} d_{1,I} = 0.028, \\ d_{2,I} = 0.03, \\ D_{11,I} = -0.005, D_{12,I} = 0.002, \\ D_{21,I} = 0, D_{22,I} = -0.003. \end{array} \right.$$

Mature parameters:

$$\left\{ \begin{array}{l} d_{1,m} = 0.07, \\ d_{2,m} = 0.08, \\ D_{11,m} = -0.008, D_{12,m} = 0.01, \\ D_{21,m} = 0, D_{22,m} = -0.013. \end{array} \right.$$

Parameters of the birth functions:

$$\left\{ \begin{array}{l} p_1 = 1, \beta_1 = 0.5, \\ p_2 = 1, \beta_2 = 0.8. \end{array} \right.$$

Maturation time:

$$r = 20.$$

Using Maple, we see that the equilibria are

$$E_0 = (0, 0), \quad E_1 \cong (3.78209, 0), \text{ and } E_2 \cong (3.98113, 2.14394).$$

We already know from section 2 that E_0 and E_1 must be unstable, and for E_2 we can easily check that conditions (19) and (20) are satisfied. Thus, it must be stable. These conclusions can be observed in Figure 7 and Figure 8. Also, they suggest that E_2 is actually globally stable.

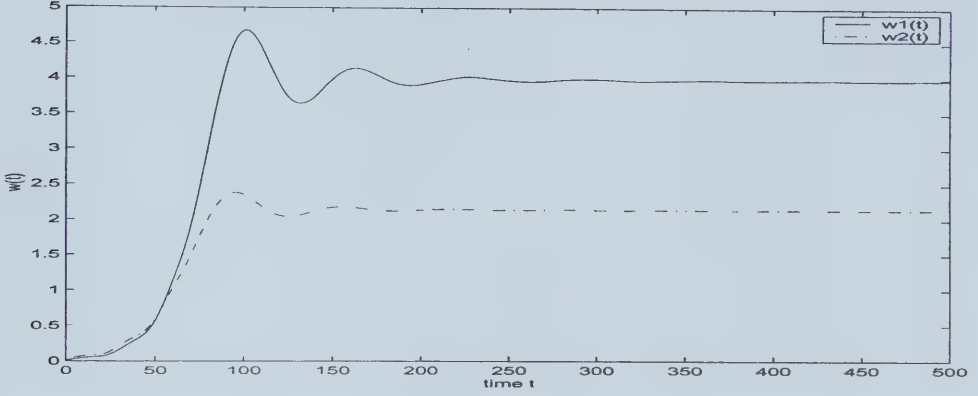


Figure 7: *Simulation 1.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (0.01, 0.02)$ for $t \in [-r, 0]$.

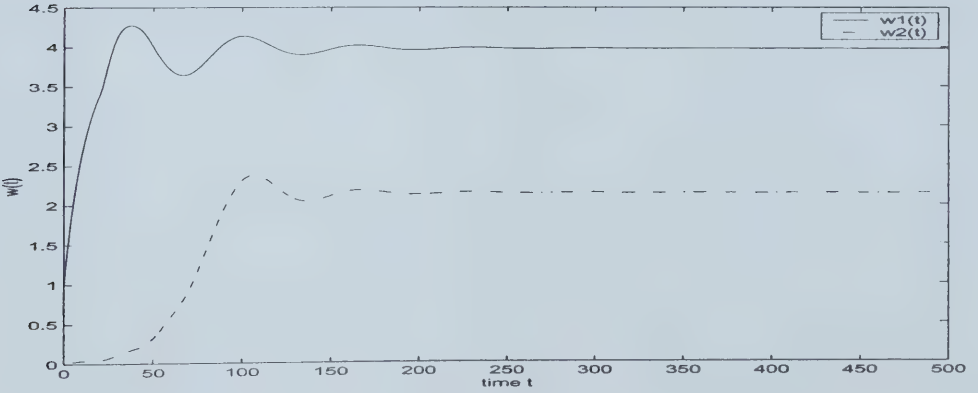


Figure 8: *Simulation 1.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (1.0, 0.01)$ for $t \in [-r, 0]$.

Although E_1 is unstable in the w_1w_2 -plane, it is actually stable along the w_1 -direction, in the sense that if $w_2(t) = 0, \forall t \in [-r, 0]$, then the solution must converge to E_1 eventually. We can see this in Figure 9 and Figure 10. Note the contrast between Figure 8 and Figure 9.

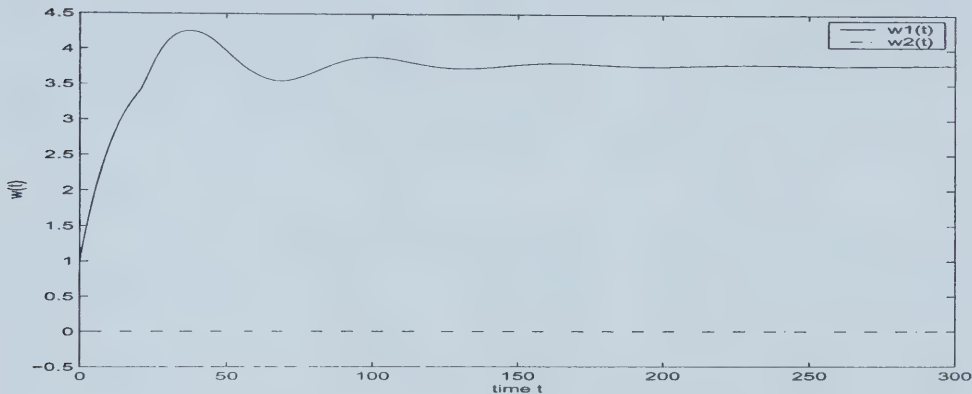


Figure 9: *Simulation 1.1:* The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (1.0, 0)$ for $t \in [-r, 0]$.

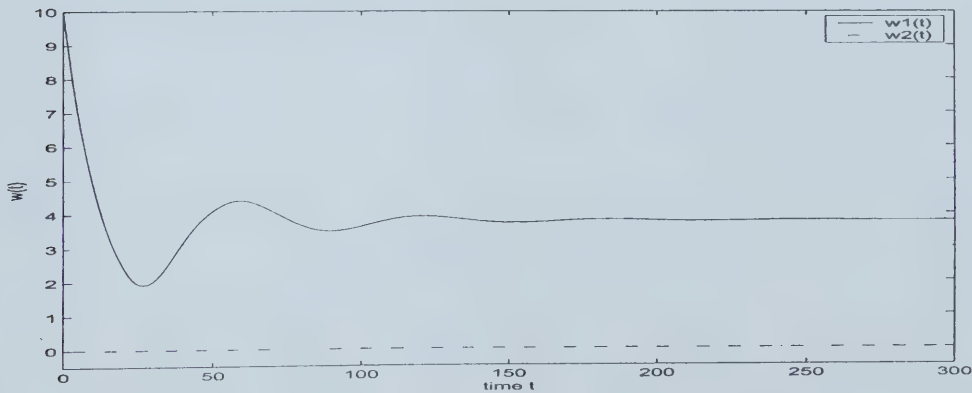


Figure 10: *Simulation 1.1:* The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (10.0, 0)$ for $t \in [-r, 0]$.

Simulation 1.2

We are going to use several simulations to verify the second part of Theorem 2.4, which is the existence of Hopf bifurcation from E_2 along the w_2 -direction. The parameters we are going to use are basically the same as those in *simulation 1*. However, this time, we will treat p_2 as a bifurcation parameter and do several simulations with different p_2 . Using Maple, we know that the first bifurcation value $\hat{p}_2 \cong 2.35912$. Recall that, as proved in Theorem 2.4, this system has infinite numbers of bifurcation values for p_2 , for example, the second and the third bifurcation value is approximately 42.21033 and 1118.87931, respectively.

Therefore, we first consider a model with the same parameters as those in *Simulation 1.1* except choosing $p_2 = 1$, which is smaller than the first bifurcation value $\hat{p}_2$, we see that the solution is not periodic in Figure 11 and the solution converges to E_2 quickly. Next, we choose $p_2 = 2.35$, which is slightly bigger than $\hat{p}_2$, and, using Maple, we find that the equilibrium $E_2 \cong (4.08018, 3.21196)$. In Figure 12 and Figure 13, we can clearly see that the solution $w(t)$ is periodic and circling around E_2 . Finally, we try $p_2 = 10$, and we see that periodic solution still exists in Figure 14. Therefore, from these simulations, we can conclude that Hopf bifurcation from E_2 first occurs at $\hat{p}_2$ and periodic solutions keep on existing after $\hat{p}_2$. Also, we should notice that the periodic behavior of $w_2(t)$ causes $w_1(t)$ to be periodic as well, which can be seen in Figure 12 and Figure 14.

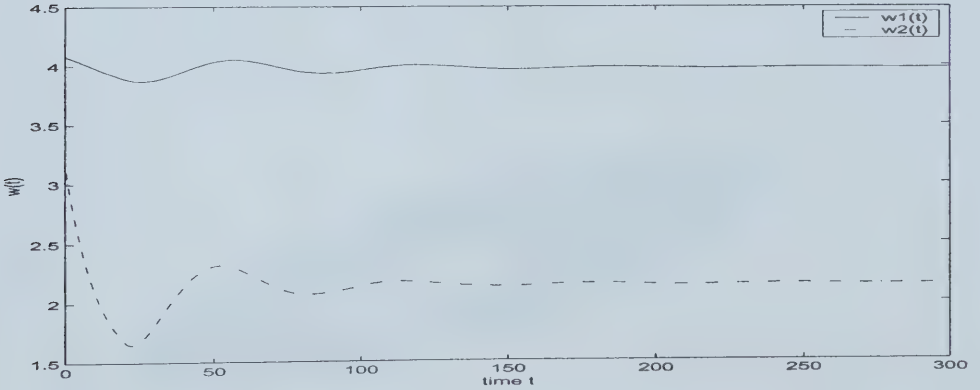


Figure 11: *Simulation 1.2*: The graph of solution $w(t)$ versus time t . Using $p_2 = 1$. Initial condition is: $(w_1(t), w_2(t)) = (4.08, 3.15)$ for $t \in [-r, 0]$.

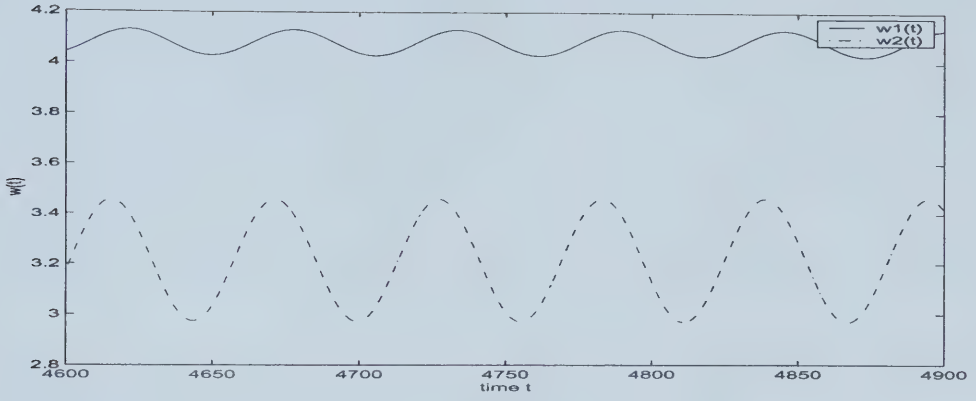


Figure 12: *Simulation 1.2*: The graph of solution $w(t)$ verses time t . Using $p_2 = 2.35$. Initial condition is: $(w_1(t), w_2(t)) = (4.08, 3.15)$ for $t \in [-r, 0]$.

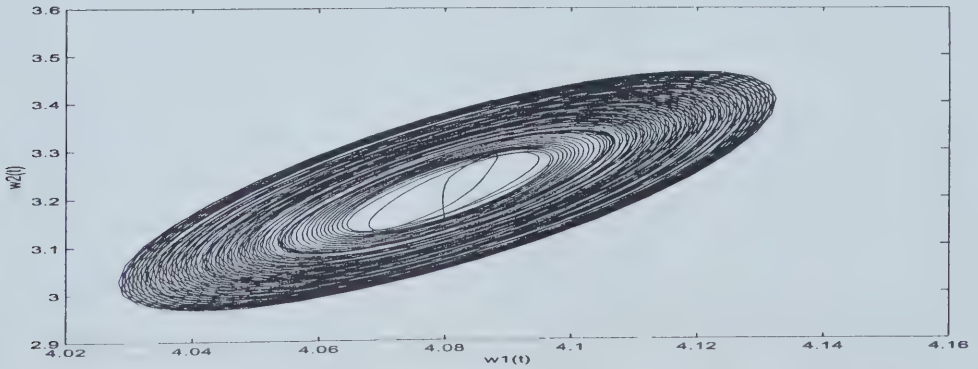


Figure 13: *Simulation 1.2*: The graph of solution $w_1(t)$ verses $w_2(t)$. Using $p_2 = 2.35$. Initial condition is: $(w_1(t), w_2(t)) = (4.08, 3.15)$ for $t \in [-r, 0]$.

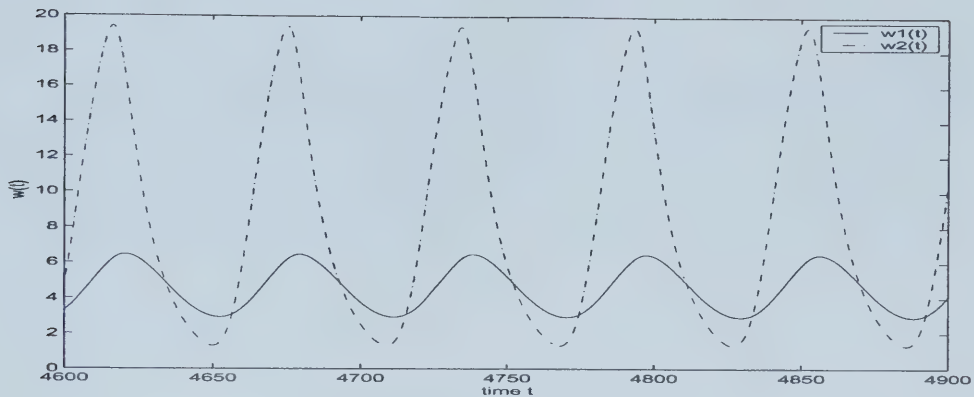


Figure 14: *Simulation 1.2*: The graph of solution $w(t)$ verses time t . Using $p_2 = 10$. Initial condition is: $(w_1(t), w_2(t)) = (4.08, 3.15)$ for $t \in [-r, 0]$.

In fact, these examples not only demonstrate the Hopf bifurcation from E_2 , they also show us what happens when E_2 is not asymptotically stable. We know that from the comment on page 11 in Section 2, E_2 will become unstable when p_2 is sufficiently big. Therefore, we now understand that when E_2 is unstable, the solutions will eventually run into a periodic orbit and oscillate around E_2 instead of converging to E_2 or blowing up. This is expectable since we know from the model equation that it is not possible for the solution to go unbounded, however, the range of the oscillation can be arbitrarily large.

Simulation 1.3

The purpose of this simulation is to demonstrate Theorem 2.3, the existence of Hopf bifurcation from E_1 along the w_1 -direction. We got the following parameters by changing those in *Simulation 1.1* and treat L as a bifurcation parameter as in Theorem 2.3. First, we will do the simulation when $L = 0.007$, which is close but slightly smaller than the bifurcation value $\hat{L} \cong 0.0070953$, then we will do the simulation when $L = 0.01$ and $L = 0.005$. Recall that $L = d_{1,I} - D_{11,I} = d_{2,I} - D_{22,I}$.

Set 1 ($L = 0.007$)

Immature parameters:

$$\begin{cases} d_{1,I} = 0.005, \\ d_{2,I} = 0.005, \\ D_{11,I} = -0.002, D_{12,I} = 0.0015, \\ D_{21,I} = 0, D_{22,I} = -0.002. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.07, \\ d_{2,m} = 0.08, \\ D_{11,m} = -0.008, D_{12,m} = 0.01, \\ D_{21,m} = 0, D_{22,m} = -0.013. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 1, \beta_1 = 0.5, \\ p_2 = 1, \beta_2 = 0.8. \end{cases}$$

Maturation time:

$$r = 50.$$

Set 2 ($L = 0.005$)

It is the same as set 1 except:

$$\begin{cases} d_{1,I} = 0.003, \\ d_{2,I} = 0.003. \end{cases}$$

Set 3 ($L = 0.01$)

It is the same as set 1 except:

$$\begin{cases} d_{1,I} = 0.008, \\ d_{2,I} = 0.008. \end{cases}$$

In Figure 15, we can see that the solution $w_1(t)$ is actually periodic and this happens when the bifurcation parameter L is slightly less than the bifurcation value

$\hat{L}$. Next, we do the simulation when $L = 0.005$, which is considerably smaller than $\hat{L}$ and we find that $w_1(t)$ is still periodic in Figure 16. On the other hand, in Figure 17, when L is larger than $\hat{L}$, we don't see the same kind of periodic solution along the w_1 -direction, instead, it converges to the equilibrium E_1 . This shows that Hopf bifurcation from E_1 occurs at $\hat{L}$.

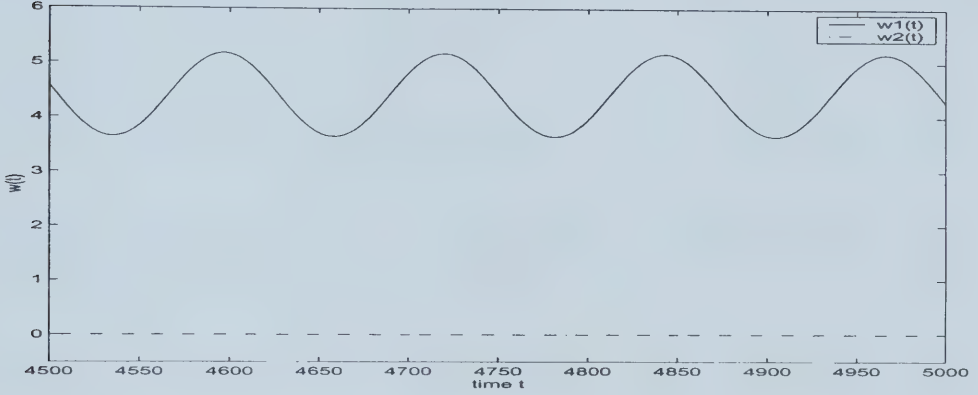


Figure 15: *Simulation 1.3*: The graph of solution $w(t)$ versus time t . Using $L = 0.007$. Initial condition is: $(w_1(t), w_2(t)) = (3.0, 0)$ for $t \in [-r, 0]$.

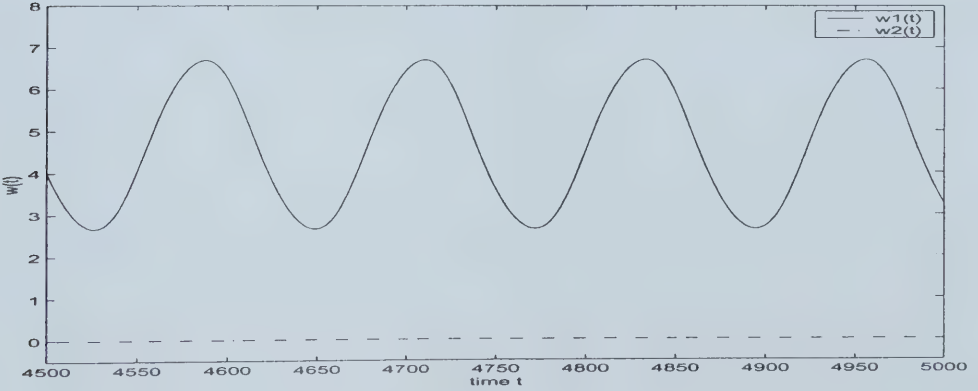


Figure 16: *Simulation 1.3*: The graph of solution $w(t)$ versus time t . Using $L = 0.005$. Initial condition is: $(w_1(t), w_2(t)) = (3.0, 0)$ for $t \in [-r, 0]$.

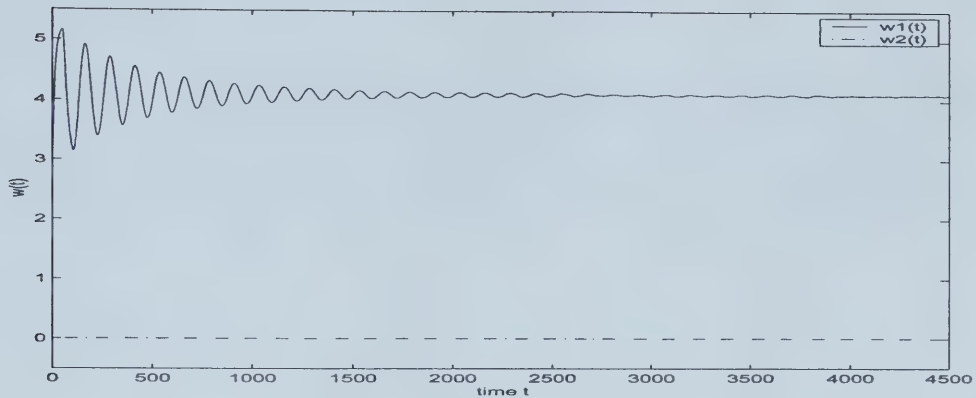


Figure 17: *Simulation 1.3*: The graph of solution $w(t)$ versus time t . Using $L = 0.01$. Initial condition is: $(w_1(t), w_2(t)) = (3.0, 0)$ for $t \in [-r, 0]$.

Simulation 1.4

We will use the following simulations to demonstrate the first part of Theorem 2.4, which is the existence of Hopf bifurcation from E_2 along the w_1 -direction. We will consider the following parameters and use p_2 as a bifurcation parameter as in Theorem 2.4. First, we will do the simulation when $p_2 = 2.61$, which is very close to the bifurcation value $\hat{p}_2 \cong 2.613$, then we will do the simulation when $p_2 = 1$ and $p_2 = 3.5$.

Immature parameters:

$$\begin{cases} d_{1,I} = 0.028, \\ d_{2,I} = 0.03, \\ D_{11,I} = -0.005, D_{12,I} = 0.002, \\ D_{21,I} = 0, D_{22,I} = -0.003. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.07, \\ d_{2,m} = 0.08, \\ D_{11,m} = -0.008, D_{12,m} = 0.01, \\ D_{21,m} = 0, D_{22,m} = -0.013. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 5, \beta_1 = 0.5, \\ p_2 = 2.61, \beta_2 = 0.8. \end{cases}$$

Maturation time:

$$r = 10.$$

In Figure 18 and Figure 19, we find that when $p_2 = 2.61$, the solution is definitely periodic in the w_1 -direction after a considerable amount of time and $w_2(t)$ converges to the equilibrium point rather quickly. Next, we do the simulation for $p_2 = 1$ and similar observations can be seen in Figure 20 and Figure 21. At last, we do the simulation for $p_2 = 3.5$ and, in Figure 22 and Figure 23, we find that there are still a lot of oscillations but the solution eventually converges to the equilibrium along both the w_1 - and w_2 -direction. This shows that Hopf bifurcation from E_2 along the w_1 -direction occurs at $\hat{p}_2$.

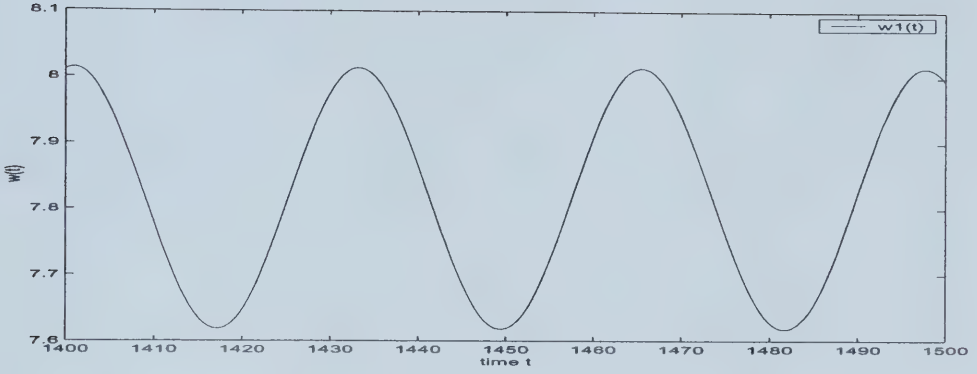


Figure 18: *Simulation 1.4*: The graph of solution $w_1(t)$ versus time t . Using $p_2 = 2.61$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

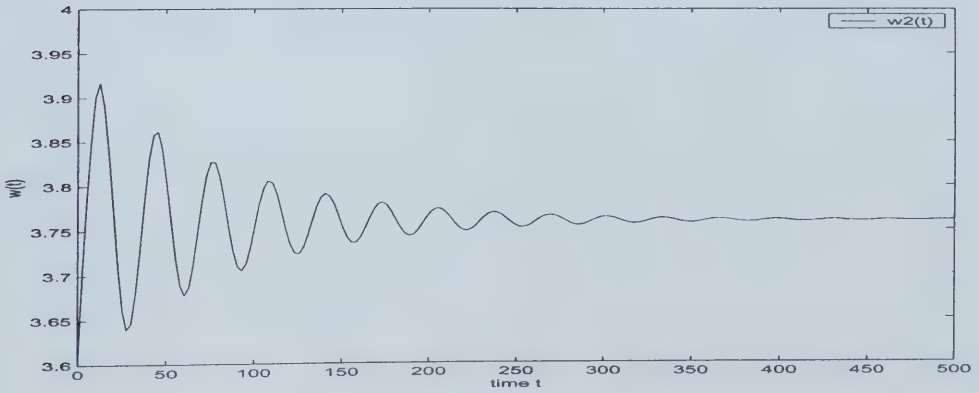


Figure 19: *Simulation 1.4*: The graph of solution $w_2(t)$ versus time t . Using $p_2 = 2.61$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

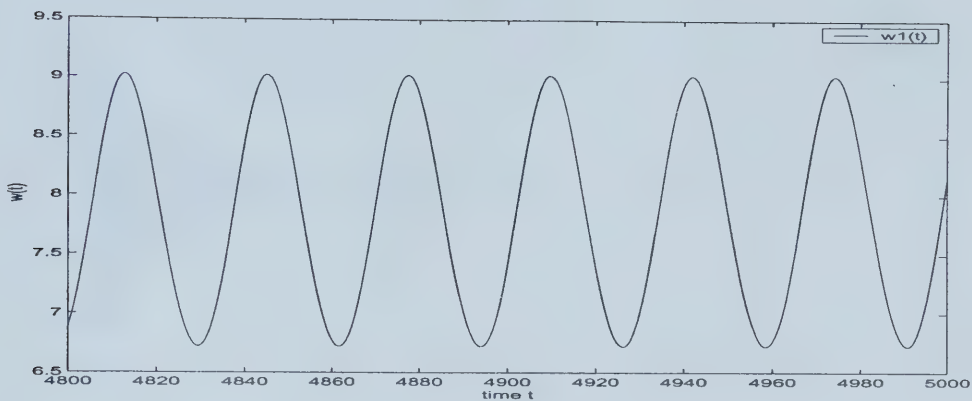


Figure 20: *Simulation 1.4*: The graph of solution $w_1(t)$ verses time t . Using $p_2 = 1$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

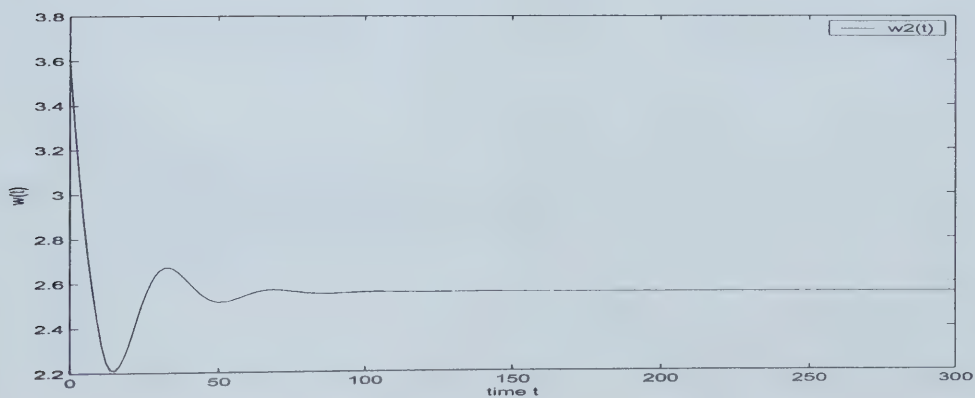


Figure 21: *Simulation 1.4*: The graph of solution $w_2(t)$ verses time t . Using $p_2 = 1$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

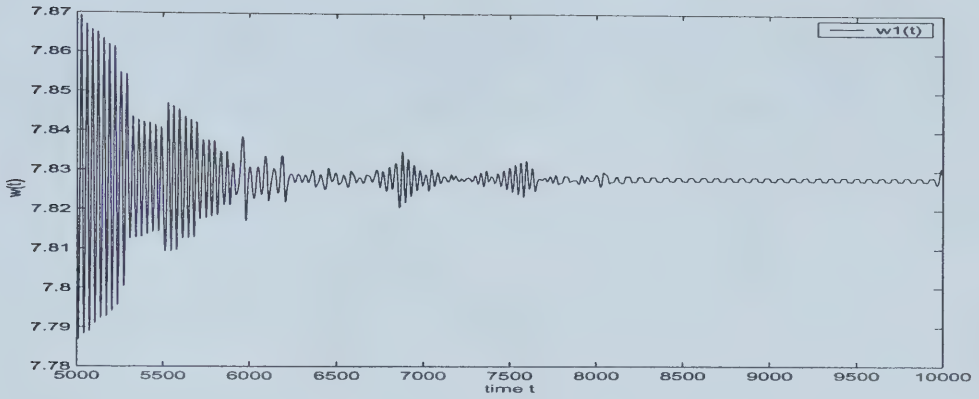


Figure 22: *Simulation 1.4*: The graph of solution $w_1(t)$ verses time t . Using $p_2 = 3.5$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

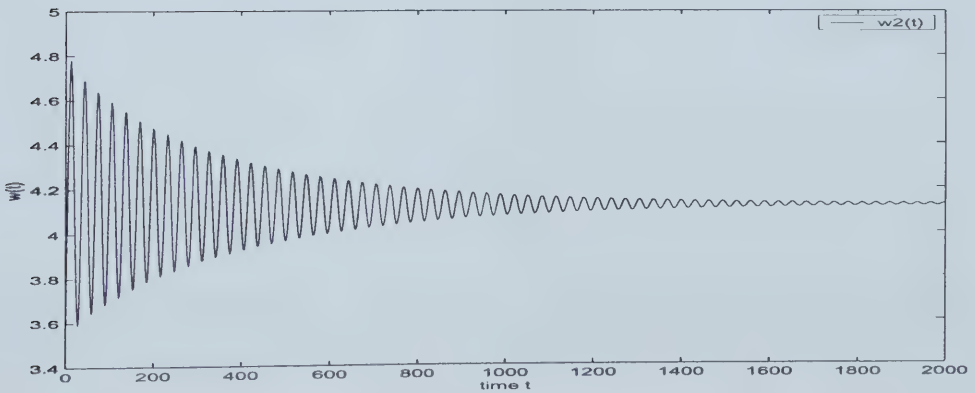


Figure 23: *Simulation 1.4*: The graph of solution $w_2(t)$ verses time t . Using $p_2 = 3.5$. Initial condition is: $(w_1(t), w_2(t)) = (7.7, 3.6)$ for $t \in [-r, 0]$.

6.2 Zero Birth Patch Model

Simulation 2.1

We do the simulation for the example that was discussed at the end of Section 4. Therefore, the main purpose of this simulation is to observe the stability of the equilibria and verify the stability results we have got before. Recall that the parameters are:

Immature parameters:

$$\begin{cases} d_{1,I} = 0.03, \\ d_{2,I} = 0.03, \\ D_{11,I} = -0.009, D_{12,I} = 0.015, \\ D_{21,I} = 0.009, D_{22,I} = -0.015. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.08, \\ d_{2,m} = 0.06, \\ D_{11,m} = -0.012, D_{12,m} = 0.008, \\ D_{21,m} = 0.012, D_{22,m} = -0.008. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 2, \beta_1 = 1, \\ p_2 = 0, \beta_2 = 0. \end{cases}$$

Maturation time:

$$r = 10.$$

Using Maple, we see that the equilibria are

$$E_0 = (0, 0) \quad \text{and} \quad E_1 \cong (2.72136, 0.79236).$$

Previously, using theorems in Section 3.2, we claimed that E_0 is unstable and E_1 is stable. These conclusions are clearly consistent with Figure 24 and Figure 25. Moreover, they suggest that E_1 is globally stable.

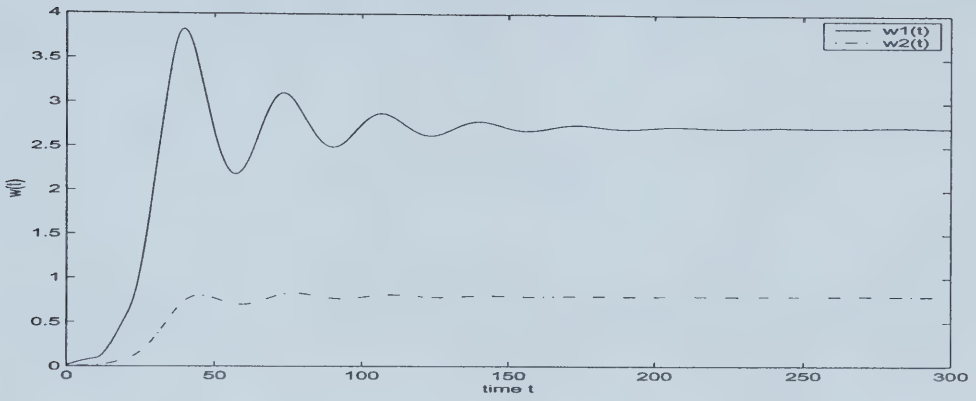


Figure 24: *Simulation 2.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (0.01, 0)$ for $t \in [-r, 0]$.

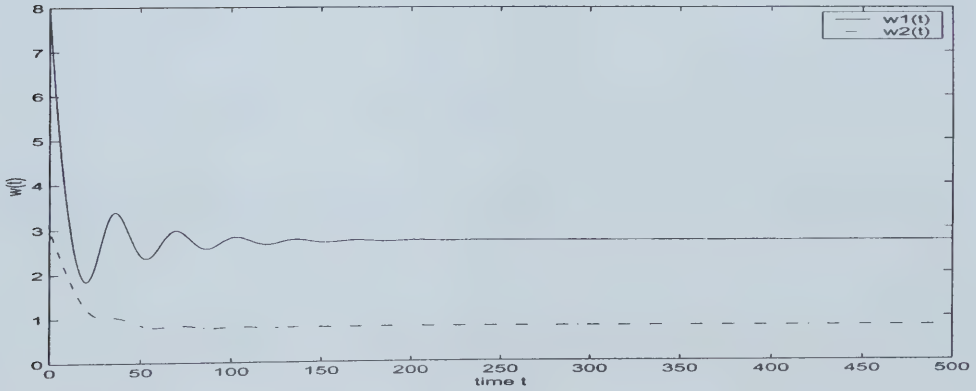


Figure 25: *Simulation 2.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (8.0, 3.0)$ for $t \in [-r, 0]$.

Simulation 2.2

We look at a case in which the death rate for both patches are relatively low and we use the parameters from *simulation 2.1* and change the death rate to the followings:

Death rates:

$$\begin{cases} d_{1,I} = d_{2,I} = 0.001, \\ d_{1,m} = d_{2,m} = 0.0015. \end{cases}$$

We see that in Figure 26 the relatively low death rates do not create any instability, the solution converge rather quickly to the equilibrium. Therefore, this suggests that the death rates do not affect the stability of the positive equilibrium.

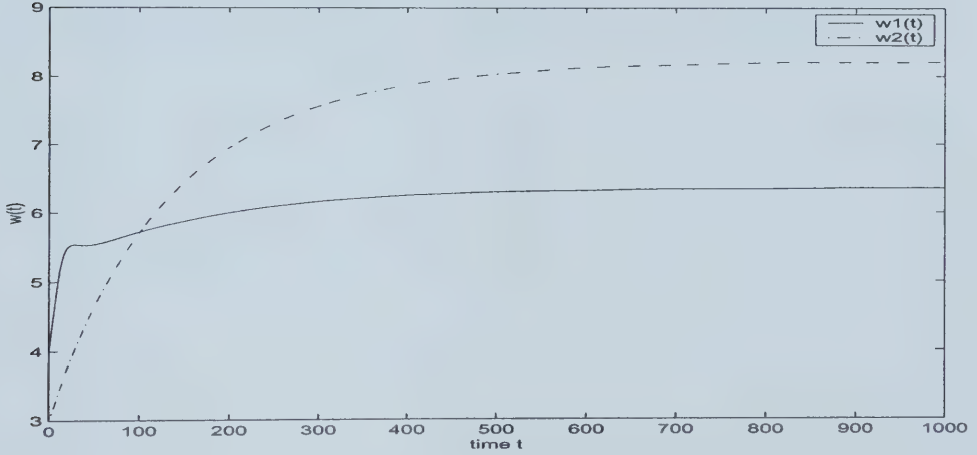


Figure 26: *Simulation 2.2*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (4.0, 3.0)$ for $t \in [-r, 0]$.

Simulation 2.3

We look at a case in which the individuals in the patch with zero growth rate cannot migrate and we use the parameters from *Simulation 2.1* and change the dispersal parameters to the followings:

Dispersal parameters:

$$\begin{cases} D_{11,I} = -0.009, D_{12,I} = 0, \\ D_{21,I} = 0.009, D_{22,I} = 0, \\ D_{11,m} = -0.012, D_{12,m} = 0, \\ D_{21,m} = 0.012, D_{22,m} = 0. \end{cases}$$

In Figure 27, we see that the solution converges to the positive equilibrium quickly. We should notice that initially patch 2 has zero population, however, its population gradually build up and is eventually stabilized by the dynamic in patch 1.

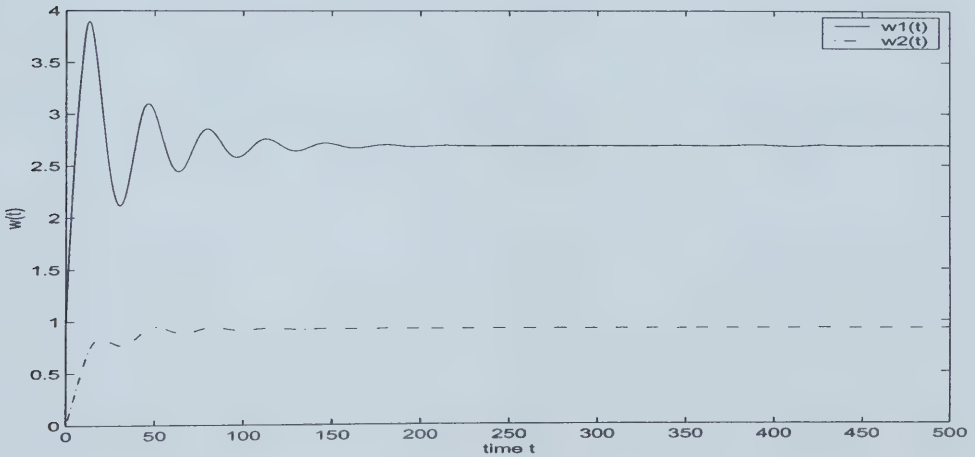


Figure 27: *Simulation 2.3*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (1.0, 0)$ for $t \in [-r, 0]$.

Simulation 2.4

We look at a case in which the individuals in the patch with positive growth rate cannot migrate and we use the parameters from *Simulation 2.1* and change the dispersal parameters to the followings:

Dispersal parameters:

$$\begin{cases} D_{11,I} = 0, D_{12,I} = 0.015, \\ D_{21,I} = 0, D_{22,I} = -0.015, \\ D_{11,m} = 0, D_{12,m} = 0.008, \\ D_{21,m} = 0, D_{22,m} = -0.008. \end{cases}$$

In Figure 28, the solution $w_1(t)$ converge to the positive equilibrium and $w_2(t)$ strictly decreases to zero. This is as expected since patch 2 has zero growth rate and has no immigrant.

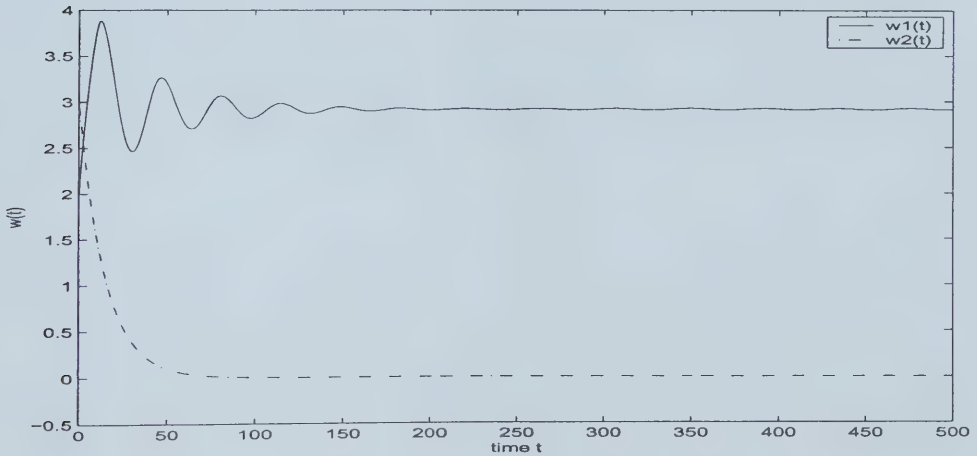


Figure 28: *Simulation 2.4*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (2.0, 3.0)$ for $t \in [-r, 0]$.

Simulation 2.5

In this simulation, we will show that when the parameter p_1 in the birth function is considerably large, it will introduce instability at the positive equilibrium. We use the parameters from *Simulation 2.1* and change the birth function parameters to the followings:

Parameters of the birth functions:

$$\begin{cases} p_1 = 5, \beta_1 = 1, \\ p_2 = 0, \beta_2 = 0. \end{cases}$$

Using Maple, we find that the positive equilibrium $E_1 \cong (3.63761, 1.05914)$. In Figure 29 and Figure 30, we can see that the solution will eventually become periodic instead of converging to the positive equilibrium. This is exactly what happens before when we do the simulation for considerably large p_2 in the birth functions in the one-way migration model (*Simulation 1.2*). In fact, when we do the the above simulation again with $\beta_1 = 20$ while keeping p_1 unchanged, we see that the instability still persists in Figure 31. Therefore, as long as p_1 is large, even the new β_1 has significantly reduce the supremum norm of the birth function, we will see instability at the positive equilibrium. Thus, we now know that p_i , $i = 1, 2$, have great influence on the stability of the positive equilibrium and when the positive equilibrium is unstable, the solutions will eventually end up in a periodic orbit. We will see a similar demonstration again in *Simulation 3.5*.

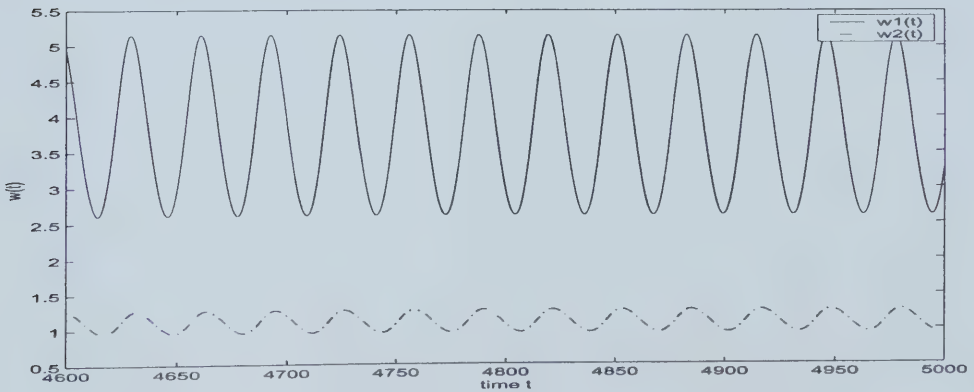


Figure 29: *Simulation 2.5*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (3.6, 1.0)$ for $t \in [-r, 0]$.

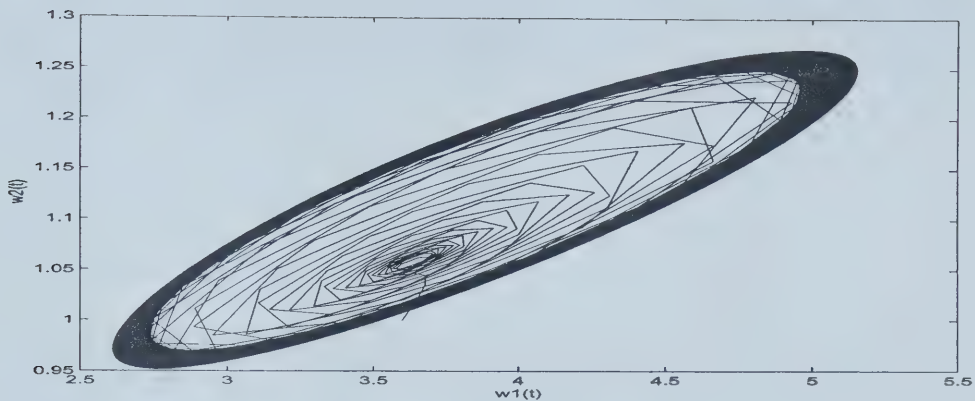


Figure 30: *Simulation 2.5*: The graph of solution $w_1(t)$ verses $w_2(t)$. Initial condition is: $(w_1(t), w_2(t)) = (3.6, 1.0)$ for $t \in [-r, 0]$.

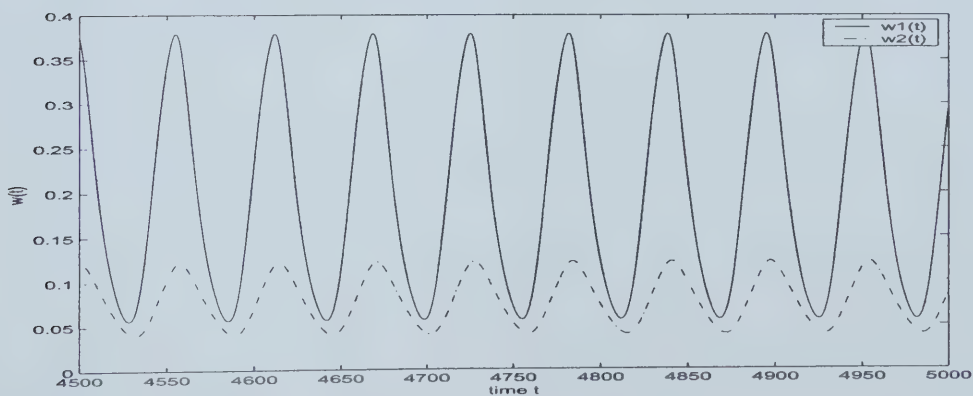


Figure 31: *Simulation 2.5*: The graph of solution $w(t)$ verses t . Using $\beta_1 = 20$. Initial condition is: $(w_1(t), w_2(t)) = (3.6, 1.0)$ for $t \in [-r, 0]$.

Simulation 2.6

In this simulation, we will further show that birth function with large supremum norm without p_1 being large does not trigger instability at the positive equilibrium. Thus, we use the parameters from *Simulation 2.1* and change the birth function parameters to the followings:

Parameters of the birth functions:

$$\begin{cases} p_1 = 1, \beta_1 = 0.001, \\ p_2 = 0, \beta_2 = 0. \end{cases}$$

In Figure 32, the solution $w(t)$ goes up rapidly at the very beginning, however, we see that it eventually converges to a equilibrium and this shows that the equilibrium is stable. Therefore, we can conclude that it is not because of the large supremum norm of the birth function that introduces the instability but the parameters p_i , $i = 1, 2$. We should notice that the parameter β_1 can significantly control the magnitude of the positive equilibrium.

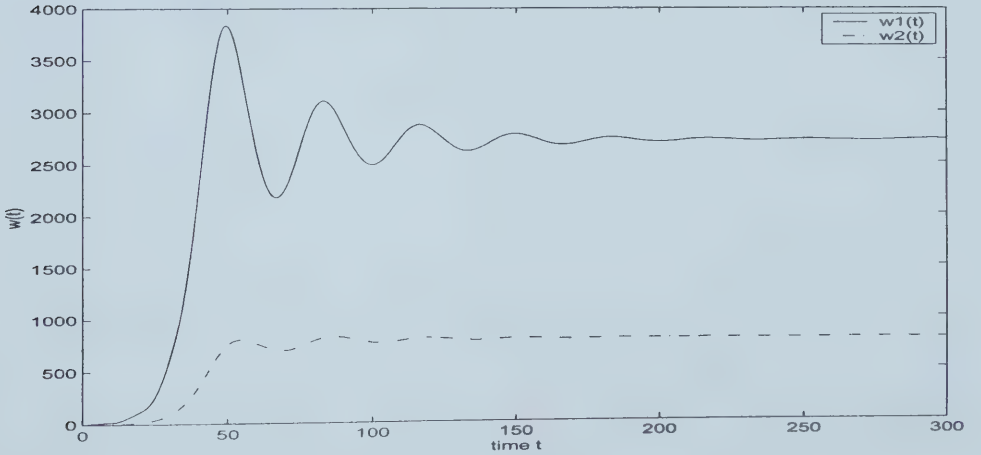


Figure 32: *Simulation 2.6*: The graph of solution $w(t)$ versus t . Initial condition is: $(w_1(t), w_2(t)) = (2.0, 1.0)$ for $t \in [-\tau, 0]$.

6.3 Immobile Immature Model

Simulation 3.1

We do the simulation for the example that was discussed at the end of Section 5. Therefore, the main purpose of this simulation is to observe the stability of the equilibria and verify the stability results we have got before. Recall that the parameters are:

Immature parameters:

$$\begin{cases} d_{1,I} = 0.03, \\ d_{2,I} = 0.04, \\ D_{ij,I} = 0, \quad 1 \leq i, j \leq 2. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.08, \\ d_{2,m} = 0.06, \\ D_{21,m} = -D_{11,m} = 0.012, \\ D_{12,m} = -D_{22,m} = 0.008. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 0.8, \beta_1 = 1, \\ p_2 = 0.2, \beta_2 = 1.3. \end{cases}$$

Maturation time:

$$r = 10.$$

Using Maple, we see that the equilibria are

$$E_0 = (0, 0) \quad \text{and} \quad E_1 \cong (1.90422, 0.88795).$$

In Section 5, we use the theorem in Section 3.3 to conclude that E_1 is stable. We can see that this is valid in Figure 33 and Figure 34, moreover, we observe that E_1 is actually globally stable and the origin is unstable.

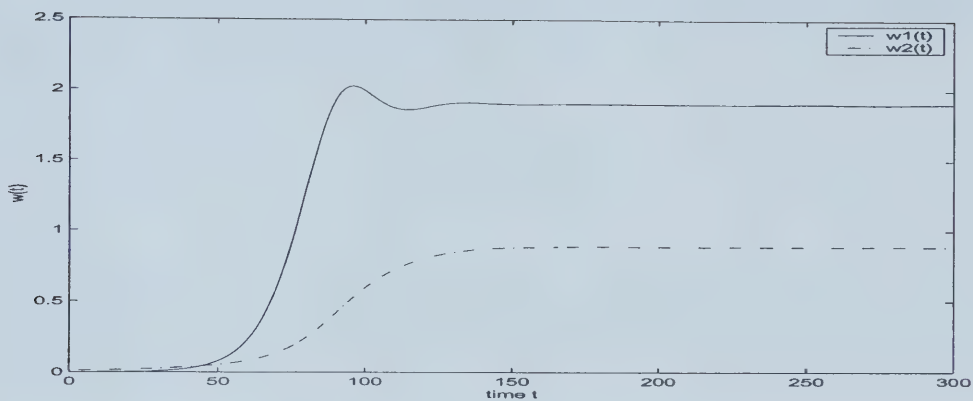


Figure 33: *Simulation 3.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (0, 0.01)$ for $t \in [-r, 0]$.

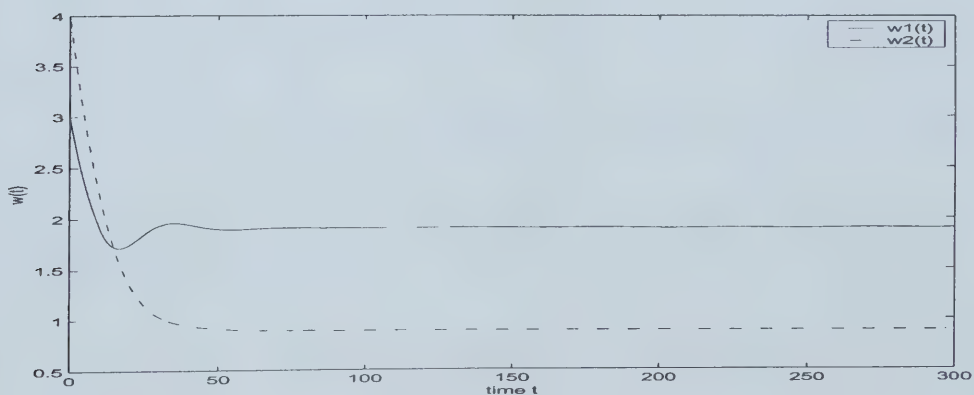


Figure 34: *Simulation 3.1*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (3.0, 4.0)$ for $t \in [-r, 0]$.

Simulation 3.2

We look at a case in which the death rate for both patches are relatively low and we use the parameters from *Simulation 3.1* and change the death rate to the followings:

Death rates:

$$\begin{cases} d_{1,I} = d_{2,I} = 0.001, \\ d_{1,m} = d_{2,m} = 0.003. \end{cases}$$

We see that in Figure 35 the relatively low death rates do not create any instability, the solution converges rather quickly to the equilibrium. Therefore, once again, this shows that the death rates do not have any impact on the stability of the positive equilibrium.

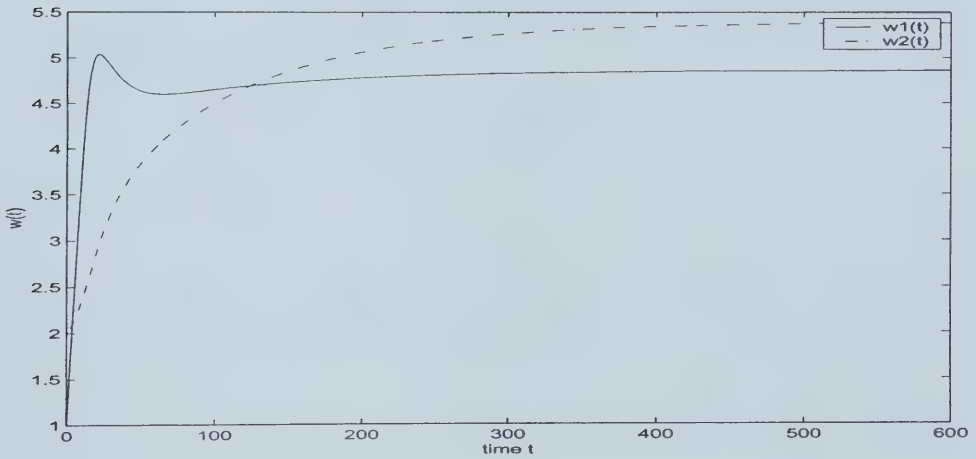


Figure 35: *Simulation 3.2*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (1.0, 2.0)$ for $t \in [-r, 0]$.

Simulation 3.3

In this simulation, we look at a case in which patch 1 has relatively low death rates and relatively low dispersal rates. We want to find out what the equilibrium state would be. We use the following parameters:

Immature parameters:

$$\begin{cases} d_{1,I} = 0.03, \\ d_{2,I} = 0.08, \\ D_{ij,I} = 0, \quad 1 \leq i, j \leq 2. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.04, \\ d_{2,m} = 0.1, \\ D_{21,m} = -D_{11,m} = 0.005, \\ D_{12,m} = -D_{22,m} = 0.013. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 0.8, \beta_1 = 1, \\ p_2 = 0.8, \beta_2 = 1. \end{cases}$$

Maturation time:

$$r = 10.$$

In Figure 36, we find that patch 1 has higher population than patch 2 at the equilibrium state. This should be expected.

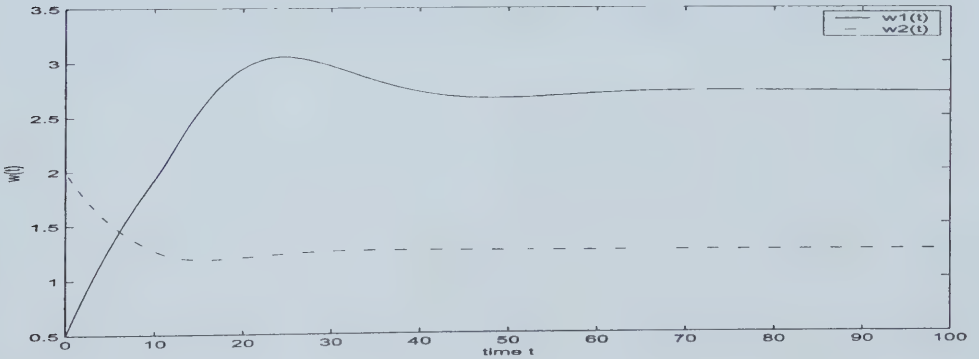


Figure 36: *Simulation 3.3*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (0.5, 2.0)$ for $t \in [-r, 0]$.

Simulation 3.4

In this simulation, we look at a case in which patch 1 has relatively low death rates and patch 2 has relatively low dispersal rates. Again, we want to find out what the equilibrium state would be. We use the following parameters:

Immature parameters:

$$\begin{cases} d_{1,I} = 0.03, \\ d_{2,I} = 0.08, \\ D_{ij,I} = 0, \quad 1 \leq i, j \leq 2. \end{cases}$$

Mature parameters:

$$\begin{cases} d_{1,m} = 0.04, \\ d_{2,m} = 0.1, \\ D_{21,m} = -D_{11,m} = 0.013, \\ D_{12,m} = -D_{22,m} = 0.005. \end{cases}$$

Parameters of the birth functions:

$$\begin{cases} p_1 = 0.8, \beta_1 = 1, \\ p_2 = 0.8, \beta_2 = 1. \end{cases}$$

Maturation time:

$$r = 10.$$

In Figure 37, we see that at the positive equilibrium state, patch 1 has higher population than patch 2. Therefore, with the knowledge of this and the previous simulation (*Simulation 3.3*), we can conclude that low death rates seem to be more important than low dispersal rates in obtaining higher population between two patches in the equilibrium state.

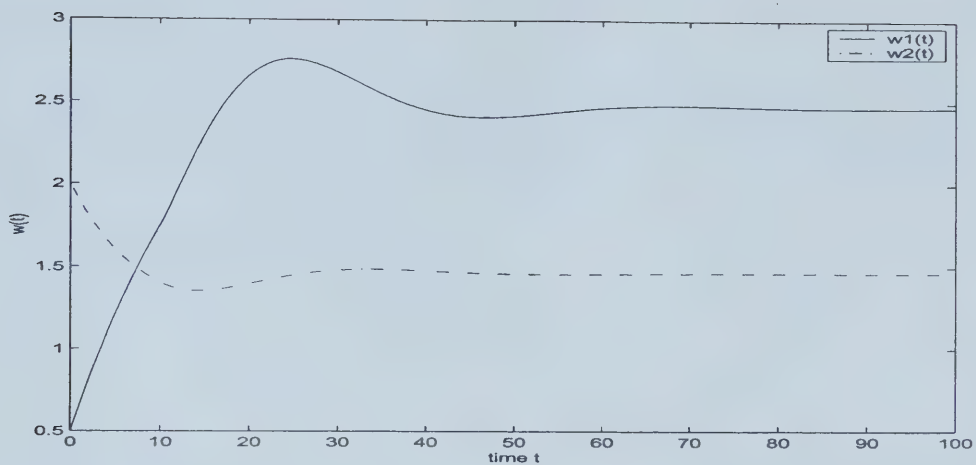


Figure 37: *Simulation 3.4*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (0.5, 2.0)$ for $t \in [-r, 0]$.

Simulation 3.5

Again, in this simulation, we will show that when the parameter p_i , $i = 1, 2$, in the birth function is considerably large, it will introduce instability at the positive equilibrium. We use the parameters from *Simulation 3.1* and change the birth function parameters to the followings:

Parameters of the birth functions:

$$\begin{cases} p_1 = 5, \beta_1 = 1, \\ p_2 = 6, \beta_2 = 1.3. \end{cases}$$

Using Maple, we find that the positive equilibrium $E_1 \cong (3.7747, 3.31124)$. As before, we see that the solution goes away from the equilibrium E_1 initially and eventually ends up in a periodic orbit as shown in Figure 38 and Figure 39. Then, we repeat the simulation with $\beta_1 = 0.001$ and $\beta_2 = 0.0013$ while choosing $p_1 = 0.8$ and $p_2 = 0.2$. Then, in Figure 40, we find that the solution converges quickly to a equilibrium point instead of turning into a periodic solution. Thus, once again, we demonstrate that large supremum norms of the birth functions are not the reason for the instability at the positive equilibrium.

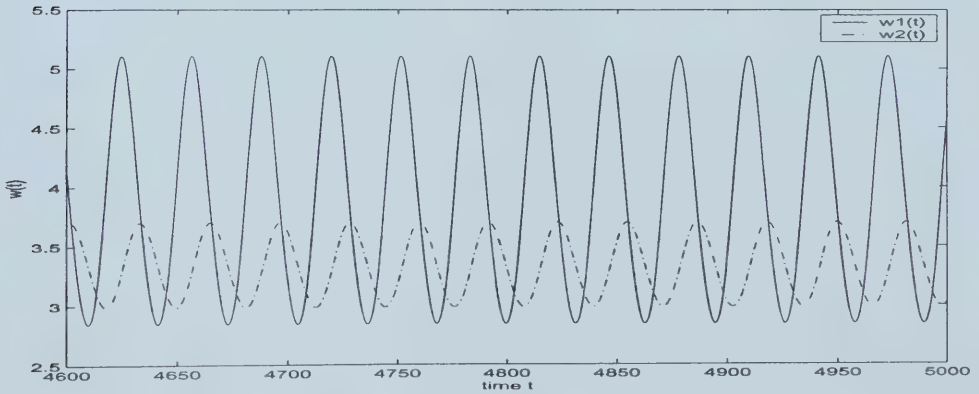


Figure 38: *Simulation 3.5*: The graph of solution $w(t)$ verses time t . Initial condition is: $(w_1(t), w_2(t)) = (3.7, 3.3)$ for $t \in [-r, 0]$.

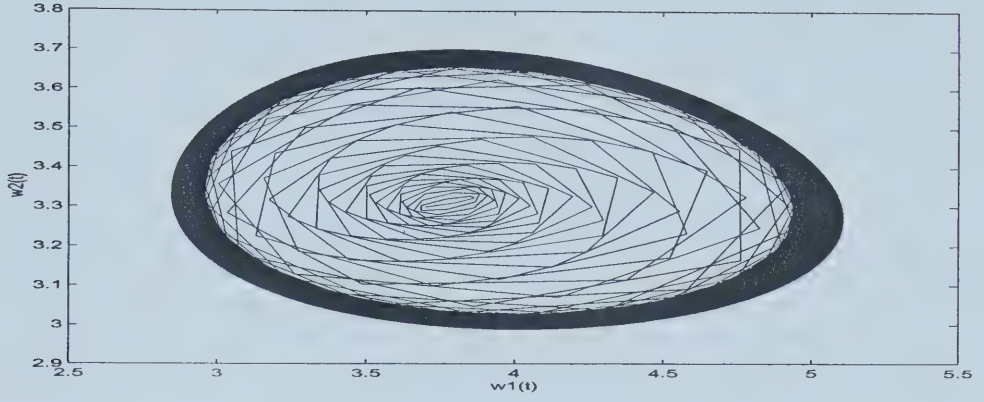


Figure 39: *Simulation 3.5*: The graph of solution $w_1(t)$ verses $w_2(t)$. Initial condition is: $(w_1(t), w_2(t)) = (3.7, 3.3)$ for $t \in [-r, 0]$.

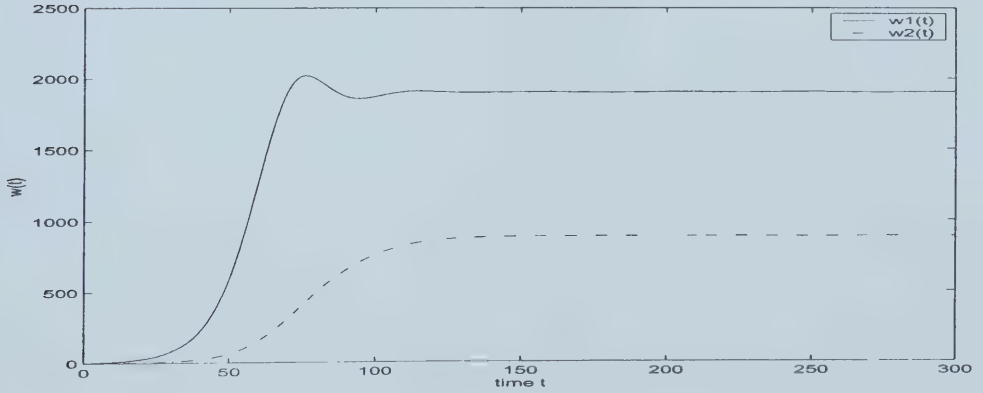


Figure 40: *Simulation 3.5*: The graph of solution $w(t)$ verses time t . Using $p_1 = 0.8$, $p_2 = 0.2$, $\beta_1 = 0.001$, and $\beta_2 = 0.0013$. Initial condition is: $(w_1(t), w_2(t)) = (2.0, 1.0)$ for $t \in [-r, 0]$.

6.4 Summary

In the first part, we did some simulations for the one-way migration model. We were able to show the existences of periodic solutions in several different cases and this verified the theorems in Section 2. In the second and the third part, we did simulations for the model, which has a patch with zero birth rate, and the model, which has all the immature being immobile. We looked at several different sets of parameters and observed the impact on the dynamics of the systems, especially the effect on the stability of the positive equilibrium. Also, we verified that the stability conclusions for the couple of examples from Section 4 and Section 5 were valid. In general, for all three models, we observed that when the positive equilibrium is stable, it is also globally stable. In the case that when the positive equilibrium is unstable, solution will eventually end up in a periodic orbit instead of wondering around or growing without bounded. Also, we discovered that the instability at the positive equilibrium is generally caused by a significantly large p_i , $i = 1, 2$, which is a parameter in the birth function, but not the magnitude (i.e. the supremum norm) of the birth function. On the other hand, the position of the positive equilibrium is greatly controlled by the parameter β_i , $i = 1, 2$, in the birth function; the smaller the β_i , the larger the positive equilibrium. In addition to this, we found that low death rates are more important than low dispersal rates in obtaining higher population between two patches in the equilibrium state.

7 Discussion

Through the study of dynamic models with maturation delay, I understood the importance of the theory of delay differential equation. Also, I found that there were a lot of complexities when considering such a model, especially when we were doing stability analysis. This was because we often end up with some very difficult transcendental equations to solve. Because of this, it made me realize that how significant it is to provide analysis for these types of equations. In this thesis, I have dealt with two types of second order transcendental equations, which arose in two different models. I successfully provided a detailed analysis that emphasize on cases in which all their roots have negative real parts. The analysis was mainly focusing on finding necessary and sufficient conditions that can be verified, at least with the help of a computer, for those cases.

A Positively Invariant for a Functional Differential Equation

We consider a system

$$x'(t) = f(t, x_t), \tag{123}$$

where $f : \mathbb{R} \times D \rightarrow \mathbb{R}^n$ is continuous and $D \subset C$ is open. It is also assumed that initial value problems associated with (123) have unique solutions. Then, from [9], we have the following theorem.

The following result is from [9]

Theorem A.1 *Assume that whenever $\phi \in D$ satisfies $\phi \geq 0$, $\phi_i(0) = 0$ for some i and $t \in \mathbb{R}$, then $f_i(t, \phi) \geq 0$. If $\phi \in D$ satisfies $\phi \geq 0$ and $t_0 \in \mathbb{R}$, then $x(t, t_0, \phi) \geq 0$ for all $t \geq t_0$ in its maximal interval of existence.*

B Fundamental Stability Results of Transcendental Functions

The following result is from [13].

Lemma B.1 *Let $f(\lambda, r) = \lambda^2 + A\lambda + B + Ce^{-\lambda r} + D\lambda e^{-\lambda r} + Ee^{-\lambda 2r}$, where A, B, C, D, E , and r are real numbers and $r \geq 0$. Then as r varies, the sum of the multiplicities of zeros of f in the open right half-plane can change only if a zero appears on or crosses the imaginary axis.*

The following result is from [14].

Theorem B.1 *All the roots of $pe^z + q - ze^z = 0$, where p and q are real, have negative real parts iff*

(a) $p < 1$, and

(b) $p < -q < \sqrt{a_0^2 + p^2}$,

where a_0 is the root of $a = p \tan a$ such that $0 < a < \pi$. If $p = 0$, we take $a_0 = \pi/2$.

The following definitions and theorems are taken from [12].

Definition B.1 *Let $h(z, w)$ be a polynomial in the two variables z and w with coefficients which may be complex,*

$$h(z, w) = \sum_{m,n} a_{mn} z^m w^n, \quad m, n \text{ nonnegative.}$$

We call the term $a_{rs} z^r w^s$ the **principal term** of the polynomial if $a_{rs} \neq 0$, and if for each other term $a_{mn} z^m w^n$ with $a_{mn} \neq 0$, we have either $r > m$, $s > n$, or $r = m$, $s > n$, or $r > m$, $s = n$.

Definition B.2 Let $f(z, u, v)$ be a polynomial in z, u , and v , which we write in the form

$$f(z, u, v) = \sum_{m,n} z^m \phi_m^{(n)}(u, v),$$

where $\phi_m^{(n)}(u, v)$ is a polynomial of degree n , homogeneous in u and v . The **principal term** in the polynomial $f(z, u, v)$ is the term $z^r \phi_r^{(s)}(u, v)$ for which r and s simultaneously attain maximum values.

Note that not all polynomials have a principal term.

Now, let $z^r \phi_r^{(s)}(u, v)$ denote the principle term, and let $\phi^{*(s)}(u, v)$ denote the coefficient of z^r in $f(z, u, v)$, so that

$$\phi^{*(s)}(u, v) = \sum_{n \leq s} \phi_r^{(n)}(u, v).$$

Also we let

$$\Phi^{*(s)}(z) = \phi^{*(s)}(\cos z, \sin z).$$

Theorem B.2 Let $f(z, u, v)$ be a polynomial with principal term $z^r \phi_r^{(s)}(u, v)$. If ϵ is such that $\Phi^{*(s)}(\epsilon + iy)$ does not take the value zero for real y , then in the strip $-2k\pi + \epsilon \leq x \leq 2k\pi + \epsilon$, $z = x + iy$, the function $F(z) = f(z, \cos z, \sin z)$ will have, for all sufficiently large values of k , exactly $4sk + r$ zeros. Thus, in order for the function $F(z)$ to have only real roots, it is necessary and sufficient that in the interval $-2k\pi + \epsilon \leq x \leq 2k\pi + \epsilon$ it has exactly $4sk + r$ real roots starting with sufficiently large k .

For the formulation of the following theorem, let us agree upon some terminology. Let $p(y)$ and $q(y)$ be two real functions of a real variable. We will say that the zero of these two functions *alternate* if each of the function has no multiple zero, if between every two zeros of one of these functions there exists at least one zero of the other, and if the function $p(y)$ and $q(y)$ are never simultaneously zero.

Theorem B.3 *Let $H(z) = h(z, e^z)$, where $h(z, t)$ is a polynomial with a principal term. The function $H(iy)$ is now separated into real and imaginary parts; that is, we set $H(iy) = F(y) + iG(y)$. If all the zeros of the function $H(z)$ lie to the left side of the imaginary axis, then the zeros of the functions $F(y)$ and $G(y)$ are real, alternating, and*

$$G'(y)F(y) - G(y)F'(y) > 0 \quad (124)$$

for each y . Moreover, in order that all the zeros of the function lie to the left of the imaginary axis, it is sufficient that one of the following conditions be satisfied:

- (a) *All the zeros of the functions $F(y)$ and $G(y)$ are real and alternate and the inequality (124) is satisfied for at least one value of y .*
- (b) *All the zeros of $F(y)$ are real and, for each zero $y = y_0$, condition (124) is satisfied, that is, $F'(y_0)G(y_0) < 0$.*
- (c) *All the zeros of $G(y)$ are real and, for each zero $y = y_0$, condition (124) is satisfied, that is, $G'(y_0)F(y_0) > 0$.*

C Properties of the Birth Function

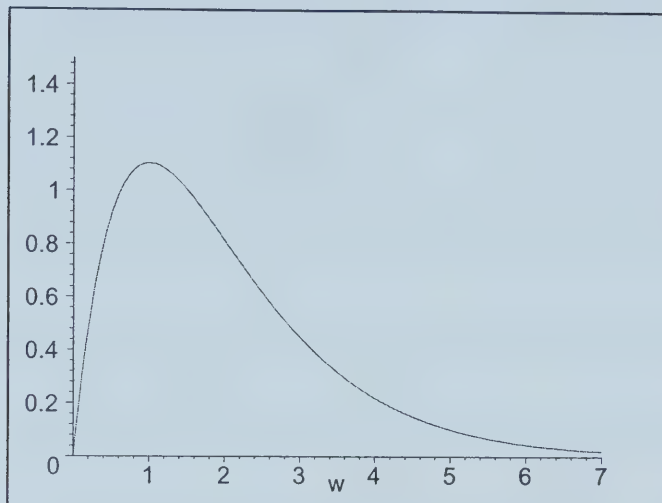


Figure 41: The graph of $b(w) = pwe^{-\beta w}$ with $p = 3$, $\beta = 1$.

Properties of $b(w)$ for $w \geq 0$:

- $b'(w) = pe^{-\beta w}(1 - \beta w)$.
- $b''(w) = p\beta e^{-\beta w}(\beta w - 2)$.
- The most positive slope is p which occurs at $w = 0$.
- The most negative slope is $-\frac{p}{e^2}$ which occurs at $w = \frac{2}{\beta}$.
- $b(w)$ is increasing on $(0, \frac{1}{\beta})$ and is decreasing on $(\frac{1}{\beta}, \infty)$. Also, $b'(w)$ is decreasing on $(0, \frac{2}{\beta})$ and is increasing on $(\frac{2}{\beta}, \infty)$. Thus, any straight line with non-positive vertical intercept will only intersect the graph of $b(w)$, ($w > 0$) at most once.

References

- [1] J.K. Hale and S.M. Verduyn Lunel, *Introduction to Functional Differential Equations*, Applied Mathematical Sciences, 99, Springer-Verlag, New York, 1993.
- [2] Y. Kuang, *Delay Differential Equations: with Applications in Population Dynamics*, Academic Press, Cambridge, 1993.
- [3] J.M. Cushing, *Integrodifferential Equations and Delay Models in Population Dynamics*, Lecture Notes in Biomathematics, Vol.20, Springer-Verlag, New York, 1977.
- [4] N. MacDonald, *Time Lags in Biological Models*, Lecture Notes in Biomathematics, Vol.28, Springer-Verlag, New York, 1979.
- [5] R.M. May, *Stability and complexity in Model Ecosystems*, Monograph in Population Biology, Vol.6, Princeton University Press, Princeton, 1974.
- [6] R.M. May, *Theoretical Biology. Principles and Applications, Second Edition*, Blackwell Scientific Publications, Oxford, 1981.
- [7] J.A.J. Metz and O. Diekmann, *The Dynamics of Physiologically Structured Populations*, J.A.J. Metz and O. Diekmann eds., Springer-Verlag, New York, 1986.
- [8] So, J.W.-H., Wu, J. and Zou, X. Structured population on two patches: modeling dispersal and delay. *Journal of Mathematical Biology*, 43 (2001), 37-51.
- [9] Hal L. Smith, *Monotones Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Mathematical Surveys and Monographs, AMS, Vol.41.
- [10] Chuma, J and van den Driessche, P., A general second-order transcendental equation, *App. Math. Notes*, 5 (1980), 85-96.
- [11] Kenneth L. Cooke and Pauline van den Driessche, On Zeros of Some Transcendental Equations, *Funkcialaj Ekvacioj*, 29 (1986), 77-90.
- [12] L.S. Pontrjagin, "On the Zeros of some Elementary Transcendental Functions," *AMS Transl., Ser.2, Vol.1*, (1955), 95-110.
- [13] Kenneth L. Cooke and Zvi Grossman, "Discrete Delay, Distributed Delay and Stability Switches," *Journal of Mathematical Analysis and Application* 86, (1982), 592-627.
- [14] Bellman, R. and Cooke, K. L., *Differential-Difference Equations*, Academic Press, New York, 1963.

- [15] W.S. Gurney, S.P. Blythe, R.M. Nisbet, Nicholson's blowflies revisited, *Nature* 287 (1980), 17-21.
- [16] L.F. Shampine and S Thompson. Solving DDEs in MATLAB, manuscript.

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